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STUDIES OF GASTROPODA.

II. FULGUR AND SYCOTYPUS.

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THE following brief account of the shell-development in Fulgur and Sycotypus, and its bearing on our knowledge of the succession of species in time is a summary of studies carried on for some years in various museums, especially the National Museum at Washington, the museums of the Academy of Natural Sciences and of the Wagner Free Institute, at Philadelphia the American Museum of Natural History, the Museum of Comparative Zoology at Cambridge, and the museum of the Boston Society of Natural History. To the officers of all these Institutions I am greatly indebted for many privileges and helpful suggestions.¹

The fulguroids are a particularly interesting group on account of their extra-limital distribution. Disregarding a few question-

¹ I wish especially to mention the names of Dr. W. H. Dall, Prof. H. A. Pillsbury, Mr. C. W. Johnson, Prof. R. P. Whitfield, Dr. L. P. Gratacap, Dr. W. Mc. M. Woodworth, Prof. R. T. Jackson, and above all, the late Professor Alpheus Hyatt, as those who have most materially assisted me in my studies of the Gastropoda.

able reports of the alleged finding of these shells in other regions, we find their geographical range in modern as well as Tertiary times to be along the Atlantic coast of North America, from the south shore of Cape Cod, to the Gulf of Mexico.

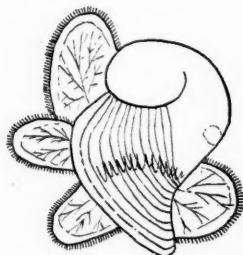


FIG. 1. *Sycotypus canaliculatus* just before emerging from the egg capsule; showing the shell, gills, heart, and large velum. $\times 13.5$.

The peculiarly restricted distribution of this group is explained by the fact, that the animal on leaving the egg capsule is without a velum. This latter, though well developed and large before hatching, (see Figs. 1 and 2) is dropped just before the animal emerges from the capsule, and after the shell is already well developed. Thus the meroplanktonic stage, which we may assume existed in the ancestors of *Fulgur* and *Sycotypus*, was apparently suppressed even in the earliest species of *Fulgur*, as otherwise the distribution would be more world-wide. Actual migration is prevented by the differences in temperature of the water and by the ocean currents. This condition of affairs has existed in this region in all probability since Miocene times.

SHELL DEVELOPMENT IN FULGUR AND SYCOTYPUS.

The earliest shell stage, *i. e.* the protoconch, may be studied easily in *Fulgur caricum* and *Sycotypus canaliculatus*. It is generally preserved in the adult shell, and may also be readily obtained from the egg capsules, particularly in the autumn, when embryos in all stages of development are found often in the same string of capsules. This protoconch consists of a single smooth volution, with no apparent markings; not even lines of growth are visible. If however a young

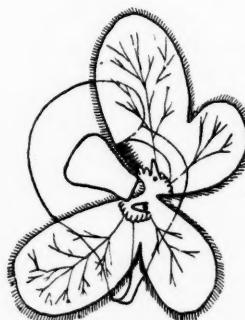


FIG. 2. *Sycotypus canaliculatus*. Ventral view of specimen Fig. 1, showing foot, tentacles, eyes, and velum just before it is lost. $\times 13.5$.

individual is taken from the egg capsule before the shell has assumed its distinctive characteristics, very faint lines of growth may be seen, as well as indistinct radiating lines. These features have been particularly observed in young *Sycotypus canaliculatus*, as noted in a previous paper.¹ In this early stage the shell is also umbilicated, and since there is no anterior canalulation as yet, this stage has the characteristics of a *Natica* shell. I have elsewhere referred to this as the naticoid stage of the protoconch, and noted its very general occurrence in gastropods.² This naticoid stage recalls the characters of early gastropods, such as *Straparollina remota* of the Lower Cambrian, which I have tentatively considered as close to the protogastropod.

The protoconch of *Fulgur caricum* generally merges into the early conch stage (the neionic³), without any visible line of demarkation between the two. Occasionally, however, such a division does exist, in the form of a strong growth line. In *Sycotypus canaliculatus* this line of demarkation appears more frequently, while in *Buccinum undatum* it is, so far as noted, a constant character. In this latter type, the change is often emphasized by an angulation in the whorl.

The neionic stage of shell growth begins with the second whorl. The outermost portion of the lip becomes gradually extended into the incipient anterior canal so characteristic of the adults of these shells. In *Fulgur* and *Sycotypus* this notch or incipient anterior canal, occurs at some distance outward from the umbilical margin of the lip, and hence as growth progresses the protoconch will have its plane of coiling tilted at an angle to that of the plane of coiling of the succeeding whorls. This gives the protoconch the characteristic oblique appearance found in many canaliculate (siphonate) types. This pattern is less pronounced in *Buccinum* and *Fasciolaria*. In consequence of

¹ Studies of Gastropoda. *Amer. Nat.* vol. 36, p. 925, fig. 8.

² *Loc. cit.* p. 919.

³ The Hyattian terminology of stages in development [ontogenetic] is: *neionic* or babyhood; *neanic* or youthful; *ephobic* or adult, and *gerontic* or senile. Each stage is furthermore divisible into 3 substages indicated by the use of the prefixes *ana*, *meta*, or *para*. The prefix *phyl-* or *phylo-* refers to the corresponding stage of racial development, *i. e.*, the phylum; thus: *phyloneanic*, *phyloephobic*, *phylogerontic*, etc.

this change of plane of coiling the second whorl partly buries the earliest portion of the first whorl or protoconch.

For about half a volution or less, the shell is smooth, although lines of growth become more pronounced. At more or less regular intervals stronger lines of growth appear (ananepionic). In the later portion of the nepionic stage (metanepionic) longitudinal wrinkles or ribs appear which characterize the ambital portion of the whorl, and may be traced upward to the suture between the two whorls. At about the same time or, in some cases, apparently earlier, faint revolving lines become visible on the shell.

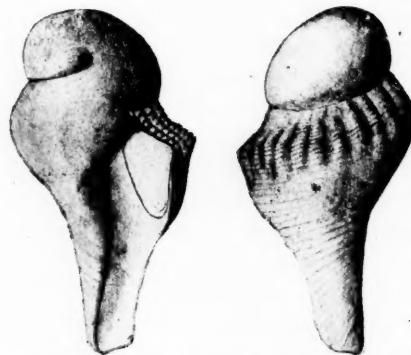


FIG. 3. *Fulgor carica*. The young shell taken from the egg capsule. $\times 11.5$.

They are nearly uniform, those on the ambitus being slightly stronger. They represent the earliest part of the primary spirals so pronounced in later stages. Almost immediately after the inception of the vertical wrinkles or ribs, an angulation appears a little above the ambitus of the whorl, which thus becomes divided into shoulder and body portion. At the same time the ribs become stronger on the angulation, where they soon assume the character of tubercles in a single row from the obsolescence of the ribs above and below the angulation. As the shoulder above the angulation broadens, two new spiral lines appear on it between the suture and the shoulder angle. These, with progressive growth, are augmented by the appearance of new ones alternately on each side of the first two. At this stage the operculum is already well developed (Figs. 3 and 4)

In *Sycotypus canaliculatus* the large velum (Figs. 1 & 2) is lost at about the time of formation of tubercles on the shoulder angle, and this may be considered the end of the metanepionic period, shortly after which the animal passes from the egg capsule. I have not examined *Fulgur caricum* at this stage, but there can be little doubt that the conditions are essentially similar. The shell-characteristics of these two types and of *Buccinum* and *Fasciolaria* at hatching are indicated in figure 18. The last or paranepionic period, distinguished by a tuberculated angulation (Fig. 4), is brought to a close in *S. canaliculatus* by the formation of the characteristic sutural canal. This, in some individuals, appears to have just begun on the lip at the period of hatching, but usually it begins only toward the end of the second volution. At this stage, the early neanic, the lines of growth are well marked and of nearly equal strength with the revolving lines, the two together giving the shell surface a reticulated appearance. The sutural canal is bounded by a strong revolving ridge, between which and the row of nodes on the angle, lies the sunken and flat or slightly concave shoulder. On this shoulder three distinct spirals are defined, at the beginning of the neanic stage, *i. e.*, the third conch volution. Shortly before the beginning of the fourth volution of the conch (the fifth counting the protoconch) a fourth spiral appears on the shoulder, close to the ridge bounding the sutural canal. A little later a fifth appears just within the line of nodes. Shortly after this, the neanic stage comes to an end, the shoulder ridge losing its nodes and continuing as a simple keel. This occurs between the fourth and fifth volutions of the conch. At the same time the inner ridge becomes less prominent, and the shoulder consequently level instead of sunken. At about this time (end of fourth volution) a sixth spiral appears on the shoulder, next to the inner ridge, and half a volution later

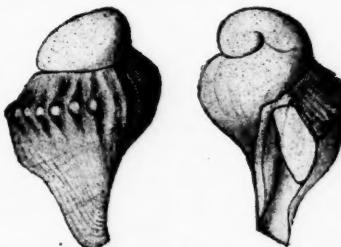


FIG. 4. *Sycotypus canaliculatus*, the young shell taken from the egg capsule. $\times 11.5$.

a seventh, next to the keel. Finally an eighth spiral appears on the sutural side before the completion of the fifth conch volution. All these spirals soon become of nearly uniform size, while a second cycle of spirals begins to appear between those of the first cycle as they diverge with the increase in width of the shoulder. A supplementary spiral also appears just within the sutural canal, next to the bounding ridge. Where these spirals are crossed by the lines of growth, short, pointed, horny spines are found on the periostracum. On the body of the shell intercalation begins much earlier than on the shoulder. In accelerated individuals intercalated spirals appear earlier on the shoulder.

Sycotypus pyrus of the modern Floridian fauna seems to be a more accelerated type. The smooth and ribbed stages are passed through quickly, occupying only about half a volution. The tubercles continue to the end of the second conch volution, after which a smooth keel succeeds. When the shell has reached the size where, in *S. canaliculatus*, the tubercles change into the smooth keel (between the fourth and fifth volutions), the keel in *S. pyrus* begins to disappear, and the curvature of the outer lip becomes uniform. In large (adult) individuals the carina has generally disappeared altogether, and the lip is rounded uniformly. This produces the "excavatus" type of lip. The canal begins in the second volution of the conch. In two old Floridian shells of *S. pyrus*, in the collection of the American Museum of Natural History, the canal becomes narrower and less pronounced in the last whorl, and in some instances it disappears altogether for a short space. In a characteristic specimen five spirals have developed by the end of the first conch volution. The sixth appears immediately after the beginning of the second volution, and the seventh begins in the third volution. Near the end of this volution intercalated spirals (of the second series) also appear, while in *S. canaliculatus* these generally do not appear until the beginning of the sixth volution. In this species the amount of embracing varies, thus changing the elevation of the spire.

ANCESTRAL SPECIES.

An immediate ancestor of *S. pyrus* seems to be *S. pyriformis* (Conrad) from the late Miocene of the Natural Well, Duplin Co., North Carolina.¹ In this species the tubercles continue nearly as long as those of *S. canaliculatus*; they become obsolete on about the fifth volution and are succeeded by a keel. The last portion of the sixth volution is rounded, as in adult *S. pyrus*. *S. pyriformis* is therefore a less accelerated type than *S. pyrus*, and fulfills all the requirements of the immediate ancestor of the latter.

The next earlier representative of the series seems to be a form from the Miocene of Faison, N. C., and probably referable to *S. canaliferus* (Conrad) Gill. The type of this species is from the early Pliocene (Waccamaw beds of South Carolina, Tuomey and Holmes), and is a more advanced type, not far removed from the recent *S. canaliculatus*. (See *Busicon canaliculatum*, Tuomey and Holmes, *Pliocene Fossil Shells of N. Carolina*, pl. 29, fig. 2). This species is considered by Dall as the ancestor of *S. canaliculatus*. It fulfills the requirements of such a relationship, in that the keel is tuberculated throughout. While *S. canaliculatus* has advanced only one stage beyond *S. canaliferus* *S. pyrus* and *S. pyriformis* have passed two stages beyond this. Therefore a species of the *S. pyrus* type only as far advanced as *S. canaliculatus*, *i. e.*, one in which the last whorl is keeled but not rounded, might be looked for in the upper Miocene. These conditions seem to be satisfied by species occurring in the late Miocene beds of Faison Mt. Pass, North Carolina.

Other specimens found in these later Miocene beds of Faison, N. C., show well the manner of formation of the sutural channel in retarded as well as primitive types. In the simplest specimen seen, a flattening appears near the suture in the third whorl of the conch. This becomes wider, more pronounced, and faintly depressed, and the shoulder has four simple revolving spirals. This condition continues to the end of the specimen (a young

¹ *Am. Journ. Conch.* Vol. 3, 1867. p. 265, pl. 20, fig. 1.

one with five volutions), while the shoulder angle at the same time retains its tubercles. In more advanced specimens the flattening, which begins earlier, is bordered by a carina arising in the third or fourth whorl of the conch, while the shoulder becomes excavated below this. The tubercles of the shoulder angle cease about a whorl later and a simple carina succeeds. In a still more accelerated specimen the flattening next to the suture is depressed on the formation of the bounding carina on the third whorl, while acceleration is also shown by the presence of intercalated spirals on the shoulder of that whorl. In the accelerated types the depressed sutural canal becomes triangular

from the development of the bounding carina into a strong posterior notch. This is emphasized, as acceleration increases, by the disappearance of the shoulder angle; which gives us, when the spire is low, the type named by Conrad *Busticon excavatus* (Fig. 5) but a type very different in appearance when high. (See *S. elongatus* Gill,

FIG. 6. *Sycotypus carolinensis*. After Tuomey and Holmes. $\times \frac{1}{4}$.



FIG. 5. *Sycotypus excavatus*. $\times \frac{1}{4}$. After Conrad.

150). Finally in these beds (Magnolia, Duplin Co., Smithsonian collection, 114540) occur specimens showing every gradation between *S. excavatus* and the extremely accelerated type described by Tuomey and Holmes as *Cassidulus carolinensis* (Fig. 6) from the Pliocene (?) of South Carolina. The "excavatus" type of aperture is, however, not confined to one line of descent, but crops out in parallel lines, *i. e.*, is a homoplastic character. This is shown by old age, or accelerated individuals of modern *Sycotypus pyrus* and by specimens referred to *S. pyrus* from the Pliocene of Shell Creek, Fla. (Natl. Mus.). These shells can therefore not be classed together as one species. Apparently *S. excavatus* led to *S. carolinensis*, and with that this branch became extinct in the Miocene. The slight development of the sutural channel in some of these specimens is probably to be explained as a case of retardation in development,

recalling the characters of the late Oligocene ancestors of the series. (See beyond.)

Another branch, which became extinct in the Miocene, is that of *S. incilis* (Conrad). This is primitive or retarded as far as the shoulder spirals are concerned, for they never reach the second cycle, but become obsolete after the third or fourth primary spiral has appeared. The change in this series is toward a progres-

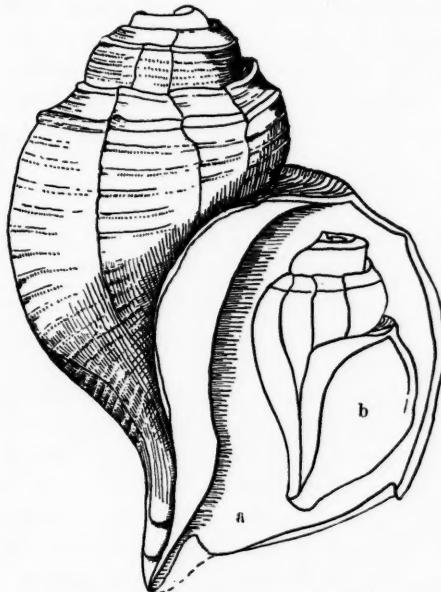


FIG. 7. *Sycotyphus incilis*. An extreme old-age type (a) and an elongate phylogorontic variety (b). From specimens in the paleontologic collections of Columbia University. $\times \frac{1}{2}$.

sive widening of the sutural canal, until, in some adults, it is wider at the lip than the shoulder. The ridge bounding it becomes very pronounced, so as to form a prominent posterior notch. This notch separates more and more from the body of the shell as the sutural canal becomes wider, until finally it occupies nearly the position which is occupied by the shoulder angle in *S. canaliculatus* (Fig. 7a). The shoulder angle becomes almost or

quite obsolete in the more accelerated individuals, thus giving the lip a rounded "excavatum" form. Here the notch made by the sutural ridge is the strongest element, having entirely replaced the original notch of the outer or keel portion. This is commonly accompanied by a looser coiling, because the succeeding whorls clasp below the middle of the preceding one instead of above it, as in *S. canaliculatus*. *S. incilis* developed in the mid-Miocene Yorktown beds, and terminated in a high-spired and short-canaled form with prominent sutural channel and obsolete shoulder angle. (Fig. 7b.) A form of this kind is not unlike in appearance to that of an old *Buccinum* in which the last whorl has been partially separated. The spirals of the shoulder are always few in number, and generally simple; indicating an off-shoot from a primitive line with few spirals, or a partial retardation affecting this feature. This small number of spirals, in *S. incilis* seems to be due to the rapid widening of the sutural channel and the consequent encroachment of the bounding ridge on the shoulder space. The latter remains always narrow, thus preventing a material increase in the number of spirals.

Apparently in the direct line of ancestry of *S. incilis* is *S. alveatus* (Conrad) (Fig. 8). This preserves

the keel throughout and has the strong ridge bordering the sutural channel. With our present knowledge we may perhaps regard *S. alveatus* as the radicle of this line, which seems to have branched off from the main line in Miocene time. The changes are towards a high spire and a profound sutural canal, terminated by an excavatum-like lip. *S. incilis* may therefore be considered as representing a phylogerontic branch in mid-Miocene time which was not propagated beyond that period.

In the Duplin beds occurs a high-spired form described by Tuomey and Holmes as *S. conradii*, but referred by Conrad to *S. incilis*. This I believe to be a distinct branch, which seems to be a derivative from the excavatus line and a parallel to *S. incilis*. In *S. conradii* the spirals remain comparatively few and



FIG. 8. *Sycothyridia alveatus*. $\times \frac{1}{2}$. After Conrad.

the whorls embrace below the middle. The sutural canal remains narrow, however, and the shell has more nearly the aspect of *S. canaliculatus*. Intermediate types connect this with *S. excavatus* and *S. canaliferus*.

The ancestral type of these branches of *Sycotypus* is probably close to *S. rugosus* (Conrad) in most characters (Fig. 9). This Mid-Miocene species retains its tubercles throughout, though these become very prominent in certain varieties and almost spine like in the later whorls. The channel already begins in the late third or early fourth whorl, hence this is no new character. The number of spirals is simple throughout, as far as observed, but there are seven of them fully formed in the fourth or fifth whorl. In some specimens the shoulder tubercles begin to unite into a strong ridge.



FIG. 9. *Sycotypus rugosus*.
× $\frac{1}{2}$. After Conrad.

In *S. coronatus* we have a form which compares in the character of the sutural canal with the ancestral type, but which has the tubercles strongly developed and the spirals intercalated at an early stage, showing acceleration in these points. Another terminal type, *S. concinnus*, Conr. has simpler spirals and a coronatus-like shoulder angle, which is however more compressed and projects more than in that species.

The ancestral type of these species of *Sycotypus* is probably to be sought in the Upper Oligocene mutations named by Dall. *tampaensis* and *perizonatus*, and referred as varieties to Conrad's *Fusus spiniger*. In the former of these, seven simple spirals occur on the shoulder and a smooth space between the suture and the first spiral in front of it. In the latter, intercalation of secondary spirals begins on the shoulder after the fifth simple one has appeared, and the smooth space next to the suture becomes depressed into a canalication. The mutation *burnsii* Dall of the Upper Oligocene, seems to be still more primitive in generally having only nodules with coarse and few spirals, and the suture scarcely channeled. It appears that the specimens classed together under the name of *Fulgar spiniger* Conrad are

not of monophyletic origin. An examination of Conrad's type from Vicksburg, Miss., in the collection of the Academy of Natural Sciences at Philadelphia shows it to have a protoconch of the *Levifusus* type. This consists of about two and one-half volutions; the apical whorl is minute, and the succeeding ones enlarge gradually. An angulation is formed by two spirals, above which the shoulder becomes gently concave. The upper spiral becomes stronger and alone forms the echinations in the later whorls. Riblets appear early after the shell has become angulated and these are soon reduced to mere tubercles. After two whorls the latter become strong enough to be called spines.

In the Lower Miocene of the Chipola River, Florida, occurs a type with true Fulgur protoconch, which has been referred to *F. spiniger*. This, together with the species referred by Dall to *F. nodulatum*, appear to be lateral branches from the main stem which led to the modern types. Conrad's *S. nodulatus* has the aspect of another extreme type of the *Levifusus* series, though it may turn out to be a true Fulgur.

At this time, as Dall has well said, the sutural canal was not a well fixed character, having but just made its appearance. It was hardly of specific and certainly not of generic value, but soon after, in the Middle Miocene, it became well established and fixed in the *Sycotypus* line of development, which henceforth became an independent branch, with only occasional rever-
sions to a faint sutural canal.

On searching for the Eocene ancestor of the fulgurs we apparently find it in a type from the Lower Clairborne of Texas, which has been identified with *Levifusus pagoda* Heilprin. This type, however, differs from Heilprin's species in having a true Fulgur protoconch, whereas *L. pagoda* has a three-whorled naticoid protoconch with gradually enlarging volutions ornamented in the latter portion by semilunar riblets. This type of protoconch is characteristic of many species of *Pleurotoma*, to which *Levifusus* seems to be closely related. But in the Texan type the obliquely elevated, swollen fulguroid protoconch is smooth for a little over a whorl and then is furnished with fine vertical ribs which merge into those of the round-whorled succeeding portion of the shell. There are at least two round whorls with

simple ribs and simple spirals, after which the shoulder flattens out and the ribs become faint toward the suture. An angulation appears on the whorl, formed at first by two strong spirals, but later, the upper becomes strongest and causes the formation of rather flattened blunt serrations. Intercalated spirals appear on the sixth whorl.

This shell, though much smaller than the Fulgurs, has all the characteristics required for an immediate ancestor. It must, of course, be separated from *Levifusus pagoda*, Heilprin, and I propose to designate it *Levifusus? harrisii*, after Professor Gilbert D. Harris, whose indefatigable labors in the Tertiaries of the Gulf region have brought together a wealth of material which may serve as a basis for further phylogenetic study. Both Dall and Harris consider *Levifusus* in the line of ancestry of *Fulgur*; the latter, indeed, regards *L. pagoda* Heilprin as the prototype of the Fulgurs. The protoconch of the ordinary form of *L. pagoda* does not satisfy the conditions of such an ancestor, but that of the Texan form does. Whether or not these two types are to be considered congeneric remains to be determined; further investigation may show that the changes from a normal naticoid type of protoconch to the oblique swollen Fulgur type occurred in this genus. We may well believe that at first the form remained unstable, oscillating between the two types, but by the time *Fulgur* had developed, that feature no doubt, had become stable. At the same time fulguroid types were probably developed from the normal *Levifusus pagoda*, the result being such types as "*Fulgur*" *spiniger* Conrad, which, as already noted, is not a true *Fulgur*. Spiniger-like forms were also developed among the true Fulgurs, the similarity of forms in both cases being explainable as an instance of parallelism. "*Fusus*" *quercollis* Harris from the Midway stage, and "*Fusus*" *rugatus* Aldrich from the Lignitic, seem to be related to the ancestors of *Fulgur*. These types, for which the generic name *Fulgurofusus* is proposed have a fulguroid protoconch, while the early whorls are almost identical with those of *Fulgur*. The adult *F. quercollis* has the *Fulgur* characters of whorl grafted upon a *Fusus* form. This type is more accelerated in that its whorls become angular as early as do those of *Fulgur*, and it is not impossible that this

type may be in direct line of ancestry of *Fulgur*. In that case *Levifusus? harrisi* cannot be considered as in the direct line of ancestry.

THE SPECIES OF FULGUR.

In turning now to typical species of *Fulgur*, we find *F. fusiformis* (Fig. 10) to be the most

primitive Mid-Miocene type. In this the simple nodules remain to the end; they are replaced by a smooth rounded keel only in accelerated or old age individuals. This species is not far removed from the Lower Miocene or Oligocene ancestor, which gave rise to the two lines of descent, *i. e.* *Sycotypus* and *Fulgur*. From *Fulgur fusiformis* on the one hand is derived the large and ponderous *Fulgur maximum* Conr. of the Yorktown beds (Fig. 13), in which the tubercles are found only in the young stage, while the adult is smooth and round-whorled. Probably a phylogenetic derivative of this is the variety *tudiculatum* from the upper bed at Alumn Bluff. In this the final whorl reaches up so as to rise slightly above the preceding ones. *Fulgur carinatum* Conr. (Fig. 12) on the other hand, is derived from *F. fusiformis* probably through *F. tuberculatum* (Fig. 11) by a consolidation of the tubercles into a continuous keel, which characterizes the last and one or more of the preceding whorls. In some

FIG. 10. *Fulgur fusiformis*, $\times \frac{1}{4}$. After Conrad.

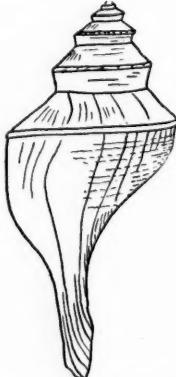


FIG. 12. *Fulgur carinatum*, $\times \frac{1}{4}$. After Conrad.



FIG. 11. *Fulgur tuberculatum*. Outline of Conrad's figure (Med. Tert. pl. 46, fig. 2) $\times \frac{1}{4}$.

specimens of *F. tuberculatum*, from St. Mary's river, Md., the nodes are replaced in the last whorl by a continuous strong and smooth keel, while in others the nodes still persist faintly on the keel of the last whorl. The more strongly spinous types of *F. tuberculatum* represent lateral radiations. In general the angular character of the whorl is retained for a brief period before the whorl becomes rounded to the maximum stage, but no true keel has been observed between the tuberculous and the smooth stages. In *Fusus*, on the contrary, a definite keel is generally formed by the consolidation of the tubercles, as in *Sycotypus canaliculatus* and *Fulgur carinatum*. In *Fusus*, a round-whorled condition follows the keel, but no spines of the *Fulgur caricum* type are known in any true *Fusus*. Similarly, a round-whorled condition follows the keel in advanced species of *Sycotypus* (*S. pyrus*, etc.). Such a condition we may expect in *S. canaliculatus* in old age types or in future accelerated descendants of the present types. Examples of *Fulgur carinatum* may yet be found with the final whorl rounded.

It appears then, that there are two branches of development in the *Fulgur* series, one leading to a keeled condition and probably never forming spines, the other to a smooth and then spinous condition. The latter branch was the successful one among the fulgurs, while the former condition succeeded in *Sycotypus*. The keeled branch occurred in the Miocene fulgurs but did not per-



FIG. 13. *Fulgur maximum*. $\times \frac{1}{2}$. After Conrad.

sist. Some of the early *Sycotypus* developed echinations by an accentuation of the tubercles, but these did not prove successful.

Hemifusus and *Melongena* represent the spinous line among the *Fusidæ*, which seems to have been equally successful with the non-spinous line of *Fusus* proper. In such types as *Hemifusus colosseus*, a strong line or spiral persists for a time after the tubercles have become obsolete. This I have formerly spoken of as a keel, but it represents merely the natural transition from tuberculous to round stage. A similar faintly carinate shoulder angle occurs again in most cases, before the spines appear.

In company with *Fulgur maximum* is a variety (var. A of Conrad) in which spines are found on the last whorl.

These spines are a new feature and are not to be confounded with the tubercles of the earlier whorls. The latter are the remains of the ribs on the shoulder angle, while the spines are periodic emarginations of the lip on the line of the shoulder angle. In the early successors of *F. maximum* these spines occur only on the final whorl, but in progressively accelerated types they come in earlier and earlier, having the appearance of being pushed back on the whorls. *Fulgur tritonis* Conrad (Fig. 14) is a type from the Mid-Miocene of Yorktown, Va., in which

spines appear after a short period of a round-whorled condition. The spines gradually increase in size until they are equal to those of the modern *F. caricum*. Two branches are met with here: *F. tritonis* Conrad with a normal anterior canal, leading to *F. caricum*; and *F. filosum* Conrad with a strong oblique fold on the anterior canal in the later whorls, leading to *F. eliceans* Montf. of the modern Fauna.

The modern *F. caricum* and *F. eliceans* are produced from their respective ancestors *F. tritonis* and *F. filosum* by an acceleration of the spinous stages, which are crowded back until the

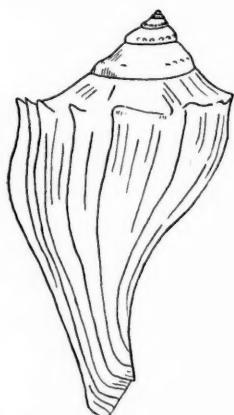


FIG. 14. *Fulgur tritonis*. $\times \frac{1}{2}$. After Conrad.

maximum stage is dropped out altogether and the spines follow immediately upon the tubercles, and even encroach upon them, thus causing a perfect gradation from tubercles to spines. *F. caricum* makes its appearance in the Waccama beds of the Carolinas while *F. eliceans* has, so far as I know, been reported only from the modern Fauna. From *F. eliceans* we finally derive the variety *candelabrum* Lam., in which there are only three or four huge spines in the last whorl.

In the late Miocene (Duplin beds of S. Carolina) and the early Pliocene (Caloosahatchee beds of Florida) a parallel series seems to have developed independently from an ancestor of the *F. fusiformis* type. In these formations occur round-whorled and spiralled shells of the *maximum* type (Fig. 13) except that they are much more strongly contracted in front of the body whorl than the Yorktown species. This gives the anterior portion of the shell a slender fusiform aspect unlike that of *Fulgur caricum*.¹ Heilprin (*Trans. Wag. Free Inst. of Sci.*, vol. 1, p. 73) describes typical *Fulgur maximum* from the Caloosahatchee beds of Florida. I have not seen these shells, which, if Heilprin's diagnosis is correct, represent the last survivors of that Mid-Miocene type. The Pliocene type is a variety of *F. rapum* Heilpr. without spines. (Fig. 15.) It is

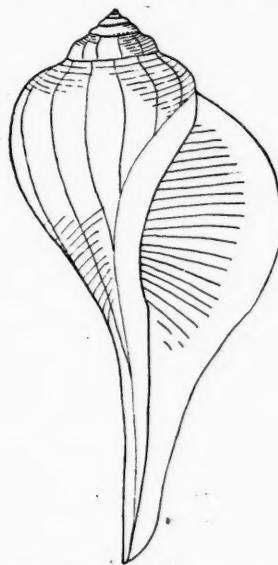


FIG. 15. *Fulgur rapum*. Smooth variety.
From a specimen in the Willcox collection.
American Mus. Nat. Hist. $\times \frac{1}{2}$.

¹ Dall states that in all the members of the genus "the females have a wide patentous canal, while the canal in male specimens is much narrower and more cylindrical." (Loc. cit. p. 115.) The difference between the specimens from the Late Miocene and Early Pliocene, and typical *F. maximum* from the Mid-Miocene, is greater than can be accounted for by sexual differences alone.

the immediate ancestor of typical *F. rapum*, and appears to connect it with *F. maximum* or *F. fusiformis*. *F. rapum* differs merely in having faint suggestions of spines on the shoulder, which has again assumed an angular outline; but this is not continuous. It represents the first stage in the development of the *caricum* features. The spines of this species are small and may be compared to the first formed portion of a spine in adult *F. caricum*, or to abortive spines in the same species. This form is probably the morphic equivalent of Conrad's *F. maximum* var. A, from the Mid-Miocene beds. More accelerated specimens with a similarly contracted form have the spines fully developed in the last whorl, and hence parallel *F. tritonis*, from which they differ only in the more slender form. This may be called *F. rapum* var. *tritonoides*. The terminal member of this branch appears to be the Floridian *Fulgur coarctum* Sowerby, which has been considered a dextral *F. perversum*, but which I believe to be of independent origin, since its ancestors are found in the Pliocene strata of the adjoining region. The interior of the shells of this series is strongly lirate, and the shells are generally thin.

Turning now to the reversed fulgurs, we find in *F. contrarium*

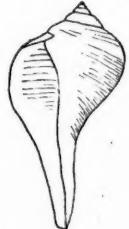


FIG. 16. *Fulgur contrarium*. $\times \frac{1}{2}$. After Conrad.

(Fig. 16) of the Late Miocene and Early Pliocene (Duplin and Caloosahatchee beds) a form comparable to the smooth variety of *F. rapum* of the same horizons. This form is knobbed in the early whorls, and rounded and smooth (except for the spirals) in the later ones. It is similar to *F. rapum* in having the same slender contracted end. It seems, from our present knowledge of the shell characters and of the geologic succession of the mutations, that the separation of the slender series into dextral and sinistral forms occurred in the Late Miocene, and that the two branches have remained separate ever since. Leidy and Willcox¹ have figured a series of reversed Fulgurs showing the gradual transition in characters from the smooth type *F. contrarium* to the

¹ *Proc. Wag. Free Inst.*, vol. 3, pl. 9 and 10.

modern spinous type, *F. perversum*. The series is exactly parallel to that leading from *F. maximum* to *F. caricum* and from *F. rapum* to *F. coarctum*, although the species correspond in form to the second rather than the first branch, as already noted. The sinistral type corresponding to *F. rapum* Heilpr. may be designated *F. obrapum* nom. nov.;¹ while that corresponding to *F. tritonoides* is Conrad's *Fulgur adversarium* (Am. Journ. Conch. vol. III, p. 185). This species is figured by Tuomey and Holmes² as *Fulgur perversum*, and by Leidy and Willcox³ as *F. contrarium* and *F. perversum* respectively. The final member of this series is *F. perversum* (Leidy and Willcox, figs. 6 and 7) from the Pliocene and modern faunas of the Gulf region. This corresponds to *F. coarctum* of the same fauna, which, as already stated, is considered by Tryon and others a dextral *F. perversum*. In Fig. 17 is represented the early neponic stage of *Fulgur perversum*.

In the Miocene marls of Cape Fear river, N. C., associated with *Fulgur filosum*, occurs a reversed type with the same characters. For purposes of designation I will apply to this the name of *Fulgur obfilosum*, nom. nov. This may represent merely a reversed condition of *F. filosum*, or it may be a member of a distinct series, developed independently and parallel to the dextral series. In its earlier stages, it is a *Fulgur adversarium* developing the characteristic fold only in the adult. This suggests that it may have been derived from that type, though the present unsatisfactory knowledge of the vertical distributions of these fossils makes it impossible to state whether or not they are in proper chronologic relation. A reversed type with the characters of *F.*

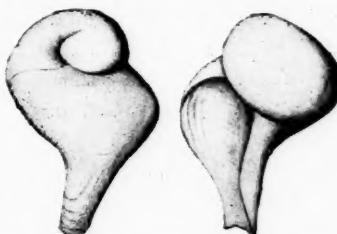


Fig. 17. *Fulgur perversum*. Young shell taken from the egg-capsule. $\times 10$.

¹ Leidy and Willcox, pl. 9 and 10, fig. 3; fig. 2 represents a *versusum* type in which a faint angularity occurs on the shoulder of the final whorl.

² *Pliocene Fossil Shells of N. Carolina*, pl. 29, fig. 3.

³ *loc. cit.*, pl. 9, 10, figs. 4 and 5.

ellicans, described by Phillippi as *F. kieneri* Phil., occurs in the modern fauna of the south coast.¹ This may be merely a reversed *F. ellicans*, but it seems more likely that it was independently derived from the reversed Miocene type just mentioned (*F. obflossum*).

The table at the end of the article indicates the probable genetic relationships of the species under discussion.

VARIATIONS IN THE SPINES OF ADULT *FULGUR CARICUM*.

Normally the spines of *F. caricum* are uniform in the adult, but individual variation is quite marked here. The final whorls of this species are generally marked by a series of color bands, or strong growth lines, which indicate a resting stage following a growth period. Each growth period begins with a non-spinous shoulder condition, and the spine begins to form only in the last half or last third of the period. At the end of the period the spine is at its maximum, and opens forward. With the beginning of the next growth period, the spine is closed anteriorly, or more rarely, is abandoned abruptly and floored over at the base, remaining open in front. Not infrequently the period is shortened, when the spine is only partially or not at all developed. This may perhaps be a pathologic condition. Sometimes the spine makes its appearance only toward the end of its normal period, and hence is small. This character, due to retardation, repeats the ancestral state of the spines in types like *F. maximum* var. A Conr. (compare *F. rapum*), where it was normal. Again, a period may be lengthened, when the spine will be larger than the normal. Such is the normal condition in *F. candolabrum*, where each period constitutes a third or a fourth of a volution.

In general, when the periods are of normal length, we find a gradual decrease in the number of periods in a volution as the shell increases in size. Thus in a number of individuals with normal periods, the average for the fifth, sixth, and seventh

¹ Kiener, pl. 9, fig. 2; Tryon, vol. 3, pl. 57, fig. 390; *F. gibbosum* Conrad. *Proc. Acad. Nat. Sci. Phila.*, 1862, p. 286.

volutions (including the protoconch) were 14, 13, and 12 respectively. Out of thirteen specimens, the average for the 6th and 7th volutions were 12 and 11 periods respectively, while 13 for the 5th volution is not uncommon. In old age or pathologic individuals the number of periods in the last portion of the final whorl becomes much greater as the periodic additions to the shell between resting stages are much shorter. Thus it appears that in normal progressive types the period increases in length as the shell increases in size, and at a rate more rapid than the increase of the shell. The number of spines on each succeeding whorl is therefore fewer. Judged by this standard, *F. eliceans* must be considered more accelerated than *F. caricum*. In *F. eliceans* the average periods for the 5th, 6th, and 7th volutions are more nearly 12, 9, and 6 respectively. Finally, in *F. candelabrum* we have extreme acceleration in this respect, as the final whorl is provided with only three periods and spines.

RELATIVES OF FULGUR AND SYCOTYPUS.

Among the near relatives of Fulgur and Sycotypus in the modern fauna we may mention *Fasciolaria* and *Buccinum*. A

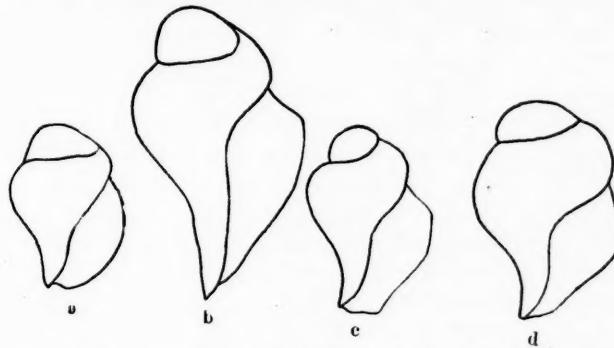


FIG. 18. Outline of young Fasciolaroid shells. a. *Buccinum undatum*, b. *Fulgur caricum*, c. *Sycotypus canaliculatus*. d. *Fasciolaria gigantea*. $\times 10$.

comparison of the early (ananepionic) shell stage of these two forms with Fulgur and Sycotypus in the same stage of development shows a very close similarity. (Compare Fig. 18.) Leav-

ing aside differences in size, we find that *Fulgur* has the longest anterior canal, *Buccinum* the shortest, while that of *Fulgur* is the narrowest, that of *Sycotypus* is the widest and most patent. *Fasciolaria* is the most ventricose of the series. In spite of these differences, there is an unmistakable family resemblance between the four young individuals, a resemblance, which in the case of *Fulgur* and *Sycotypus* is retained even in the adults. In *Buccinum undatum* spirals appear in the metanepionic stage, and ribs at a later period. In *Fasciolaria gigantea* ribs appear first (Fig. 19), the spirals afterwards. This therefore seems to be nearer to *Fulgur* in which the same order of succession of features obtains. It is therefore evident, that we must look to the Mesozoic fasciolaroid shells for the ancestors of these types.

The development of plications on the columella has been shown by Dall to be due to a relative retreat of the muscle of

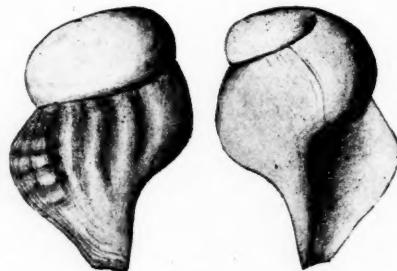


FIG. 19. *Fasciolaria gigantea*? Young shell taken from the egg capsule. $\times 10$.

fixation from the aperture, and the consequent crowding and folding of the mantle. This feature appears in a large number of phyletic series, and must be regarded as a secondary acquisition. In the fasciolaroid ancestors of the present types, such plications could not have existed, since they do not occur in *Fulgur* and *Sycotypus*, nor in the young *Fasciolaria*. We know too little about the Cretacic forms at present to determine what species are in the line of ancestry of the types under consideration. *Pyropsis* or *Pyrifusus*, both of which are well repre-

sented in the Atlantic coast Cretacic, may represent the Miocene progenitor, both having so far as I have been able to ascertain, the characters requisite for such ancestry. These may lead on the one hand to the Eocene levifusoid ancestor of the Fulgurs, and on the other hand to *Fasciolaria* through such forms as *Odontofusus*, with but a single columellar plication.¹

Fusus, *Hemifusus* and *Melongena* are not directly related to *Fulgur*. *Fusus* at least existed before *Fulgur*, having already acquired its highly accelerated protoconch in the Eocene. *Fusus* seems to be an Old World type, which did not reach the American coast until Post-Eocene time, so far as indicated by evidence now available.² *Hemifusus* is an accelerated descendant of *Fusus*, with fulguroid form,³ while *Melongena* is a phylogenetic terminal member of that series. Thus it appears that the *Fusidae* and the *Fasciolaridae* (the latter with branches leading to *Fulgur* on the one hand and to *Buccinum* on the other) have been distinct since pre-Eocene time, and that their common ancestor must be looked for in the Cretacic if not earlier.

I am well aware that to class *Buccinum* and *Fulgur* with *Fasciolaria*, and *Melongena* and *Hemifusus* with *Fusus*, subordinates lingual dentition to shell characters. The odontophores of *Fusus* and *Fasciolaria* are similar, and different from those of the other genera mentioned. In these again the type of dentition is similar, though minor significant differences occur. It seems to me that where the shell characters point the other way, mere similarity of dentition is insufficient to establish relationship, but must be explained rather as parallelism.

We know nothing of the lingual dentition of the Tertiary and earlier species, and but little of that of modern types. Furthermore we know nothing of the changes, if any, which the dentition undergoes in the development of the animal and so cannot use lingual ontogeny as index of genetic relationship. The den-

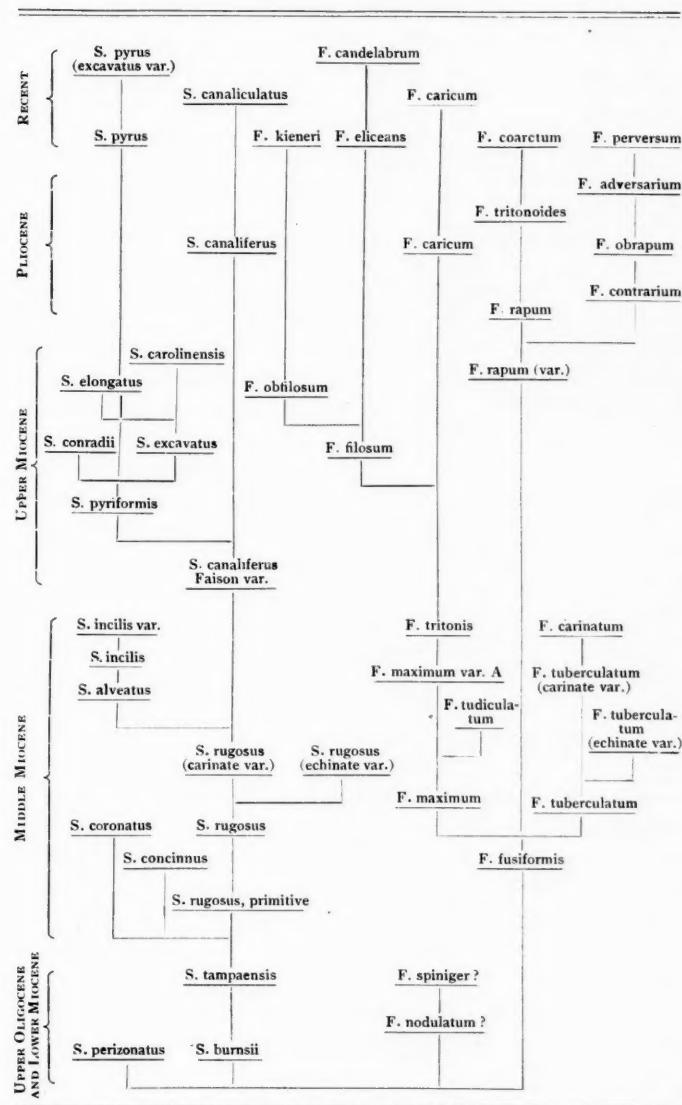
¹ See Whitfield: *Gastropoda and Cephalopoda of the Raritan Clays and Green-sand Marls of New Jersey*. Monograph 18 U. S. Geol. Survey.

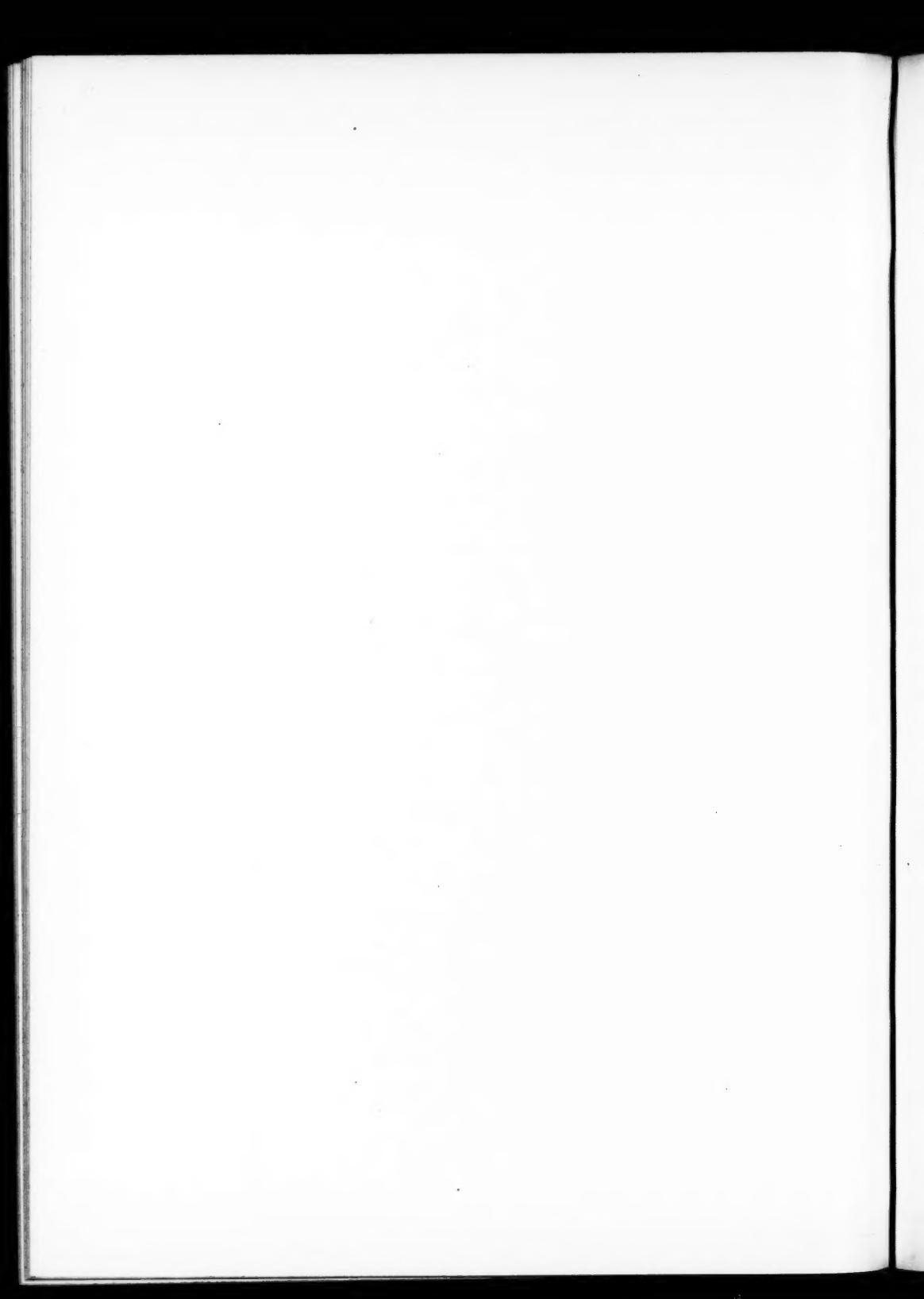
² The American Eocene species of *Fusus* so far described do not belong to that genus. See Grabau: *American Naturalist*, vol. 36, p. 922.

³ For illustration of protoconch and early conch of *Hemifusus* see Grabau *loc. cit.* p. 921, fig. 5.

tal apparatus of *Buccinum* and *Fulgur* is very similar, and that of *Hemifusus* and *Melongena* is nearly identical. In both groups, the outer members or marginals of the adult odontophore bear each one large and one or more small denticles, while the median is supplied with small denticles only. In *Fasciolaria* and in *Fusus* so far as known, the marginals are furnished with numerous nearly equal denticles. If we assume that in the ancestral type both marginals and median had one or at the most only a few denticles, it is easy to see how the multidenticulate type of modern *Fasciolaria* may be developed along one line, and the similar type of modern *Fusus* along a parallel line. It is also easy to see, that the heterodenticulate types of modern *Buccinum* and *Fulgur* could branch off from the primitive *fasciolaroid* ancestor, by the accentuation of the outer denticle of each marginal. Again the simple *melongenoid* type could branch off from the primitive *fusoid* type, and develop by a similar accentuation of the outer denticle. I see therefore no sufficient reason in the similarity of odontophores for the present classification of these genera, and instead of uniting *Fulgur* and *Hemifusus*-*Melongena* in one family, and *Fusus* and *Fasciolaria* in another, I feel that the development of the shell characters show very clearly the close relationship of *Fusus* and *Hemifusus*-*Melongena*, and of *Fasciolaria* and *Fulgur*, with *Buccinum* not far removed.

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TABLE OF THE GENETIC RELATIONSHIPS OF THE SPECIES OF *FULGUR* AND *SYCOTYPUS*.



CONTRIBUTIONS FROM THE ZOOLOGICAL LABORATORY OF THE
MUSEUM OF COMPARATIVE ZOOLOGY AT HARVARD
COLLEGE. E. L. MARK, DIRECTOR.—NO. 144.

ON THE STRUCTURE OF THE OUTER SEGMENTS
OF THE RODS IN THE RETINA OF
VERTEBRATES.

ARTHUR D. HOWARD.

SOME forty years ago the structure of the rods in the retina of vertebrates excited a lively interest and received the attention of many skilled observers, whose researches were directed principally to the rods in the amphibians because of the advantage offered by the large size of these organs. Good summaries of these early investigations have been given by Hoffmann ('73-'78), and by Krause ('92).

From the first of these sources the following description of the outer segment of the rod is taken. The outer segment is composed of a highly refractive substance staining black with osmic acid. In form it is cylindrical with a hemispherical, slightly bulging, distal end. Under high magnification its outer surface is seen to be marked by parallel striations which deviate from a strictly longitudinal course only in that they are very slightly spiral. This appearance is due to superficial furrows alternating with ridges. The form of the outer segment may thus be well compared to that of a column with a slightly spiral fluting. In addition to the longitudinal striations, transverse bands are present at regular intervals. These are surface indications of a plate structure. The plates of which the outer segment is composed are constant in thickness for a given species and show little variation even in the whole vertebrate series. They are held together by a cement lying between their approximated faces. This cement is affected rapidly by certain reagents and by its swelling causes a characteristic disintegration of the outer segment into disks. This disintegration occurs earlier at

the distal end of the segment than at the proximal one, the difference having been attributed to a protecting sheath over the latter. The presence of an axial fiber, as maintained by Ritter and others, was discredited because of much negative evidence.

In contrast to this general view Krause ('92), whose comparative studies included particularly *Rana* and *Salamandra*, maintained that the outer segment consisted of a bright "Grundsubstanz," in the periphery of which fibrils were imbedded and twisted in so close a spiral that they gave the appearance of transverse striations, thus producing a condition favorable to apparent transverse fracture. Greeff (:00, p. 103), however, has recently expressed himself in favor of the older view that the outer segment consists of a series of plates with an enveloping sheath. "Jedes Aussenglied besteht 1. Aus einer *Hülle* (Mantelschicht, Rinde, Haut) und 2. einem aus Plättchen und Zwischensubstanz gebildeten *Inhalt*." This view is also accepted by Levi (:01).

Bernard (:00, :01), who has published an account of the embryonic as well as of the adult rods in amphibians, has maintained that these structures are protrusions from a syncytial retina and that each rod is a delicate protoplasmic vesicle traversed by a reticulum which eventually becomes condensed into the axis of the rod by the absorption of a colorless refractive and amorphous matter from the pigment cells. Thus even among recent investigators much difference of opinion exists as to the structure of the vertebrate rods.

The progress made in the study of the rods in vertebrates during the last twenty-five years stands in considerable contrast with that made in the investigation of the terminal optic organs of invertebrates. In the arthropods, for instance, the rhabdomes, the analogues of the rods and cones of vertebrates, were supposed by most of the earlier writers to have been formed by secretion, and in fact Watase ('90) went so far as to compare them with surface cuticula. Their fibrous character, however, was observed by Patten ('86) and others and it was demonstrated by Parker ('95) that in the crayfish the fibrils composing them are neurofibrils, and that the substance of the rhabdome is more correctly described as differentiated living material like the

contractile substance of a muscle fibre, than as a secretion. This view that the rhabdome is composed of neurofibrils has been greatly extended among the invertebrates by the recent work of Hesse (:00, :01).

Since in some crustaceans the rhabdomes are not only fibrous but are composed of plates not unlike the so-called plates in the rods of vertebrates, it is natural to ask whether the rods in vertebrates may not also be fibrous, and with this question the present paper is chiefly concerned. The ease with which frogs could be obtained at all seasons and the comparatively large size of their rods led me to investigate the retinas of these animals and I chose in particular the common leopard frog, *Rana pipiens* Schreber, as a favorable species.

For a satisfactory study of the rods it was necessary to free them from their surrounding pigment. This was done in the usual way by keeping the animal two or three hours in the dark. In such "dark frogs" the retinal pigment completely withdraws from the region between the rods into the bodies of the retinal pigment cells.

Of the various methods for obtaining unwrinkled retinae the following was used with success, and I know of no other which preserves the eye in as natural a condition as this does. Frogs kept the usual length of time in the dark were etherized, their hearts were exposed, and fixing fluid was injected into their arteries as in ordinary injections to demonstrate the arterial system. The fluids used were Vom Rath's picro-platino-osmo-acetic mixture, $\frac{1}{2}\%$ osmic acid, corrosive-acetic mixture, and Perényi's fluid.

The last two penetrated most successfully. The osmic preparations were only partially successful, for, owing apparently to the rapid constriction of the blood vessels, a smaller amount of the fluid reached the interior of the eye than by the other methods. After injection, the whole head was immersed in the fixing fluid and the eyes were not opened until they were more or less fixed. Eyes thus prepared were embedded in paraffine and cut for longitudinal or transverse sections of the rods. The sections were stained in Heidenhain's iron-hæmatoxylin, Böhmer's hæmatoxylin, Mayer's hæmacalcium, and by Kupffer's and

Bethe's methods for neurofibrils. Preparations were also made by the cover-glass method for blood technique. This is well adapted for experimenting with a large number of reagents and stains, and has the advantage of insuring immediate fixation.

The examination of material prepared in the ways enumerated gave evidence of a well marked axial core in the outer segment of each rod. This core was seen in both longitudinal and transverse sections of rods fixed in the various fluids already mentioned and measured about one fourth the diameter of the rod. It took none of the stains which I have tried with the possible exception of picric acid. It is probably the structure long ago seen by Dreser ('86) and recently identified by Bernard (:01, p. 465) as the condensed reticular portion in the axis of the rod. Its relative thickness precludes the possibility of its being the so-called fibre of Ritter, if in fact this fibre exists. At present I do not wish to express any opinion as to the exact nature of this core.

As previously stated the substance of the rods has been variously described as lamellar, spirally fibrous, etc. Since rods prepared by different methods showed much difference in structure, it was necessary to study fresh ones as a means of interpreting what was seen in the preserved preparations. But under the ordinary microscope the substance of fresh rods appeared to be almost homogeneous and I was, therefore, obliged to seek other means of studying these bodies. The problem thus resolved itself into a search for conditions which would bring out optical differentiation in an object which under ordinary circumstances seemed optically homogeneous. Polarized light seemed the most likely means, for, if the rods are fibrous not only ought this to be open to determination by a polarizing microscope, but it ought also to be possible by the same means to ascertain the direction of the fibrils.

A polarizing microscope was used with a powerful artificial white light and a gypsum interference plate inserted between the Nicol prisms. The prisms were placed at such an angle to each other as to give an interference color of a sensitive violet of the first order. With the apparatus thus set up fresh preparations of the retina more or less teased out were examined.

In such preparations fields may easily be found containing detached rods with their longitudinal axes lying in various directions.

Outer segments lying parallel to the α axis of the gypsum plate, $\pm 45^\circ$ to the cross-hairs, showed a bright yellow color, while those at right angles to this were bright blue. The colors of an individual rod could be reversed by turning the preparation so as to bring the rod into a line at right angles to its former position. The inner segments of the rods are not highly refractive. These observations were made on the rods of *Rana pipiens* but I have also tested the outer segments of the rods or cones, as the case may be, in the mudpuppy (*Necturus*), turtle, snake, lizard (*Anolis*), guinea pig, mouse, and ox, and with wholly confirmatory results.

This definite reaction demonstrates that the substance of the outer segments is positively doubly refractive or anisotropic, *i. e.*, as regards their optical properties the outer segments have axes of maximum elasticity at right angles to their lengths. To obtain an immediate basis for comparison I made similar tests of other tissues. Thus bundles of naked axis cylinders from the inner surface of the vertebrate retina gave light reactions exactly like those given by the outer segments of the rods and the same was true of striped muscle fibres from the crayfish, frog, and ox as well as of connective tissue fibres from the ligamentum nuchæ. The rhabdomes from the compound eye of the crayfish were, however, negatively anisotropic, but when it is remembered that the fibrous structure of these bodies is at right angles to their length instead of being parallel to it as in all the other bodies tested, this apparent exception disappears. Since the neuro-fibrils are known to run lengthwise the axis-cylinders of nerves and since naked axis-cylinders and the outer segments of the rods give the same color reactions in the polarizing microscope, I believe I am justified in concluding that fresh outer segments of the rods of vertebrates like axis cylinders of nerve fibres possess a longitudinal fibrillation.

The color reactions just recorded are directly opposed to Krause's conception of the rods as made up of spirally twisted fibrils. Such a structure would give color reaction the opposite

to those actually seen, for the fibrils would be nearly at right angles to the longitudinal axis of the rod. Nor do these reactions favor the view held by Bernard (:01) that the rods are protoplasmic vesicles filled with an amorphous refractive substance, for the material is not amorphous but gives evidence of longitudinal fibrillation. Patten's ('98) hypothesis that the outer segments are made up of minute fibrils at right angles to their longitudinal axes is also inconsistent with these observations.

Although the evidence I have advanced cannot be said to be opposed to the generally accepted view that the rod is made up of many disk-shaped plates, I am not inclined to place so much emphasis on this as some have done. I have obtained abundant evidence for the presence in fresh rods of transverse bands about equal to each other in thickness and held together by an intermediate substance of different optical behavior. But I have not found the evidence for the disintegration of a rod into disks at all convincing. There were certainly frequent instances of transverse breaking, but it was seldom clear cut and there were often signs of longitudinal splitting and of spreading at broken ends.

I believe we have in the rod certain conditions analogous to those of striped muscle fibres. Both bodies are positively refractive, both possess a transverse lamellar arrangement of optically differing substances, and under the action of certain reagents both are said to break into transverse segments.

The structure of the muscle fibre is essentially fibrillar notwithstanding its transverse fracture and I believe the structure of the outer segment of the retinal rod to be in this respect like that of the muscle fibre.

Having given the evidence for the longitudinal fibrous structure of the rods as I have found it by the use of polarized light, I wish to discuss some contradictory results already recorded as having been obtained by this method. Valentin ('62) investigated with polarized light a large number of animal tissues including the rods of the retina and the axis cylinders of nerves, and, as the following quotations show, he found that the reactions of these two bodies were not similar but opposite. "Die nähere Verfolgung des Gegenstandes zeigt, das die optische Axe der Längsaxe der Nerven parallel geht, man also hier

einen wahrhaft negativen Körper vor sich hat und die ganze Erscheinung nur von dem Marke herührt" (Valentin, '62, p. 123). "Man könnte theoretisch annehmen, das die Stäbchen an und für sich nicht anders, als die markigen Nervenfasern wirken" (p. 136). "Jene (Stäbchen) wären aber wahrhaft positiv und das (Nerven) Mark von diesen wahrhaft negativ" (p. 136).

It is thus evident that Valentin believed that the optical axes of the rods and of the nerve fibres were not in agreement but were at right angles to each other, and this opinion was accepted by Max Schultze ('67), Krause ('92),¹ and Greeff (:00).

It is not easy to account for Valentin's statement that the axis cylinders of nerves are negatively anisotropic unless we assume that in consequence of the imperfect knowledge of nerve structure at his time he has recorded the reaction of the medullary sheath, which is negative, instead of that of the axis cylinder. Valentin's work was done on *Torpedo marmorata* and shows that his observations were made almost entirely upon medullated nerves. It is quite evident that what he refers to as sheaths of the nerve must have been the positively reacting connective tissue of the peripheral nerves, for he makes no mention whatever of the brilliantly conspicuous medullary sheath as such. He does, however, speak of pressing out the retina of a frog with a cover-glass and finding fibres which he considers to be parts of the optic nerve. These, he states, also showed negative reactions, but there is no certainty that what he described were really optic nerve fibres.

In my tests of nerves I found medullated fibres unsatisfactory objects for clear demonstration of optical properties in the axis cylinder, because of the strong predominance of the reaction color of the medullary sheath. The non-medullated fibres from invertebrates (crayfish) were more satisfactory, but even here the presence of the positive Schwann's sheath, though comparatively thin, made conclusive observation out of the question for the color of the sheath was projected on the less strongly reacting axis.

¹"Die Aussenglieder sind ferner positiv doppelbrechend, die optische Axe liegt in ihrer Längsrichtung und es ist bemerkenswert das sie sich entgegengesetzt wie das bekanntlich negativ Nervenmark verhalten." (Krause, '92, p. 159.)

It was, therefore, necessary to use nerve fibres without protective coverings. The naked axis cylinders radiating from the entering optic nerve in the fibre layer of the retina, met this requirement. In order to get a clear demonstration of these, I made tests upon the retina from a perfectly fresh ox eye where the large size of the eye made manipulation comparatively simple. In this case there was little difficulty in identifying the radiating bundles of nerve fibres which were readily distinguishable from small blood vessels and other structures of a fibrous nature. The bundles of naked axis cylinders proved to be distinctly *positive*, thus agreeing with the rods and I am consequently forced to conclude that in some way Valentin's observations were in this respect erroneous.

Summary. The outer segments of the rods in the retina of the frog contain each an axial core that differs from the peripheral substance, but the exact nature of this core has not yet been made out. The outer segments, as demonstrated by the use of polarized light, are positively anisotropic and agree in this respect with the axis cylinders of nerves. These outer segments therefore, give evidence of containing longitudinal fibrillæ. Since they also show in the fresh state a transverse banding, their structure is in some respects not unlike that of a cross-striped muscle fibre in that in addition to a cross banding they also possess a longitudinal fibrillation.

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VERNACULAR NAMES OF ANIMALS.

EDWIN W. DORAN.

THE interests of popular science demand the introduction of some system in writing the common, or vernacular, names of animals and plants. There is not only a great lack of uniformity among authors as to the correct form of these names ; but in case of some approach to an agreement with regard to certain forms, often the agreement is without reference to the principles that underlie the formation of such words.

From an examination of many thousand names of animals it appears that only about ten per cent. of the names consist of a single word ; about thirty per cent. consist of two or more words which should be written in separate form ; about sixty per cent. consist of two or more words which should be written in compound form. (Not all of these should have a hyphen, however, as will be shown later). What names should be included in this sixty per cent. is a problem upon the solution of which this paper is designed to shed some light.

There are those who say the solution of the problem lies in abolishing the use of vernacular names entirely, and using in their stead the more exact technical names. There is little hope of getting any except the most rigidly scientific, to adopt for everyday use the unfamiliar forms derived from foreign languages, no matter how exact they may be. Vernacular names always have been in use and no doubt always will be. No one expects to live to see the day when we shall discard the familiar names of dog, cat, rabbit, squirrel, cow, and sheep, and use in their places the high-sounding though exact names derived from the Latin or the Greek. If we retain these common names, — household words, — we may expect also to retain such other names derived from them, as prairie-dog, wildcat, jack-rabbit, ground-squirrel, sea-cow, and mountain-sheep. Then we are likely to distinguish still farther between the many closely-related forms by using Missouri prairie-dog, American wildcat, white-

tailed jack-rabbit, striped ground-squirrel, Dall mountain-sheep, etc.

These terms are less exact for English-speaking people than the corresponding technical ones simply because of the confusion that has always existed in writing them; because of the many names that have been applied to the same animal. The same confusion would exist with reference to the technical names but for the carefully prepared synonymies. I believe that I am the first¹ who has thought it necessary to prepare a synonymy of the vernacular names of animals.

Some writers appear to have an antipathy for the much-abused little character, known as a hyphen. This seems to be true also of many printers and publishers. As one writer puts it, "A hyphen affects some printers very much as a red rag does an angry bull"; hence they omit the greater number of hyphens in a manuscript. Many writers on science relegate to the printer or to their amanuensis such details of manuscript-revision and proof-reading, owing to a lack of authorities on the subject.

Dr. J. A. Allen says²: "If the use of the hyphen could be permanently regulated by the formation of a set of rules, how great a boon would be conferred upon writers, and particularly upon editors! As, however, the use of the hyphen varies within wide limits, in accordance with the radically different rules enforced by editors and publishing houses, from its practical non-use to its employment to connect remote elements into a compound word, there is little hope of securing a uniform system of hyphenization in the construction of bird names. . . . In publications which allow the hyphen its time-honored function, great diversity is met with in just the class of cases to which Dr. Doran has called attention."

Here is the difficulty. Every writer has some system of rules which he follows in compounding words (provided he gives any attention to the subject at all); but too often these rules are formulated without regard to language-principles or reason.

¹ The author has in preparation a synonymy of all the vernacular names of vertebrates. Mr. Robert Ridgway many years ago suggested the need of something of this kind for the names of birds.

² *The Auk*, Jan. 1903, discussing my article on Vernacular Names of Birds.

Some have not taken the trouble to reduce their rules to tangible form or to a system, and thereby get rid of their inconsistencies.

Now, I believe that a system of rules may be formulated and in accordance with the established principles of the English language, by means of which we may be rid of the present chaos in compounding the vernacular names of animals.

The writer has previously attempted this for certain groups of animals¹ and in this paper the discussion is extended so as to include all classes of vertebrates and the insects.

Before formulating a set of rules for compounding the vernacular names of animals, it is necessary to give attention to a few well-established general principles — principles which are recognized by all the great masters of English, though expressed concisely by few writers. In fact, the literature of the subject is very meager, and only within the last twenty years has there been any serious attempt to evolve a system of writing such words.

The *Standard Dictionary* lays down three general principles for compounding English words,² the second of which is as follows: "Abnormal association of words generally indicates unification in sense, and hence compounding in form." In accordance with this principle I submit the following rules for compounding the vernacular names of animals.³ Following each rule are given numerous examples taken from the different groups of animals to show the application of the rules. The first rule is more general than the rest, and to some extent includes the others.

Write in compound form, —

1. Any pair of names or words in joint arbitrary use; as, leaf-roller, black-nosed dace, four-toed salamander, red-bellied snake, blue-throated lizard, soft-shelled turtle, whippoorwill, polecat.

¹ See 'Entomological News,' Nov. 1902, for a discussion of the vernacular names of insects, and 'The Auk,' January, 1903, previously cited, for a similar treatment of the names of birds.

² Consult also the works of F. Horace Teall on compounding English words.

³ These rules are intended to apply to insects and vertebrates only, but will be found serviceable for all forms.

2. A general name used with any other name prefixed for specification denoting,
 - a. Food or prey ; as, potato-beetle, spawn-eater, chicken-snake, duck-hawk, rice-rat.
 - b. Host ; as, horse-fly, dog-flea (chiefly parasites).
3. A general name used with any other name prefixed for specification denoting,
 - a. Similarity ; as, mole-cricket, alligator-gar, cricket-frog, garter-snake, box-turtle, turkey-vulture, fox-squirrel.
 - b. Habit ; as, army-worm, pilot-fish, rattlesnake, snapping-turtle, butcher-bird, flying-squirrel.
 - c. Habitat ; as, house-fly, brook-trout, tree-frog, water-moccasin, fence-lizard, land-tortoise, wood-duck, prairie-dog.
 - d. Characteristic ; as, scale-insect, sword-fish, spade-foot frog, horn-snake, spine-tailed lizard, map-turtle, song-sparrow, musk-ox.
4. A phrase consisting of an adjective and a noun together used as a mere name, formed by writing (generally in solid form),
 - a. An adjective with the name of an animal ; as, whitefish, blacksnake, redbird, wildcat.
 - b. An adjective with the name of some characteristic feature of the animal ; as, longsting, blackfin, bluetail (lizard), yellowlegs, bighorn.

I feel safe in affirming that the foregoing rules are so simple that anybody can apply them ; that they are sufficiently comprehensive to include all names of the groups indicated ; and that they are in accord with reason, language-principles, and the usages of the highest authorities.¹ I admit that the rank and file of investigators in any particular department of science may vary widely in usage from these rules, or any other set of rules that might be formulated.

All the vernacular names can not be found in any one diction-

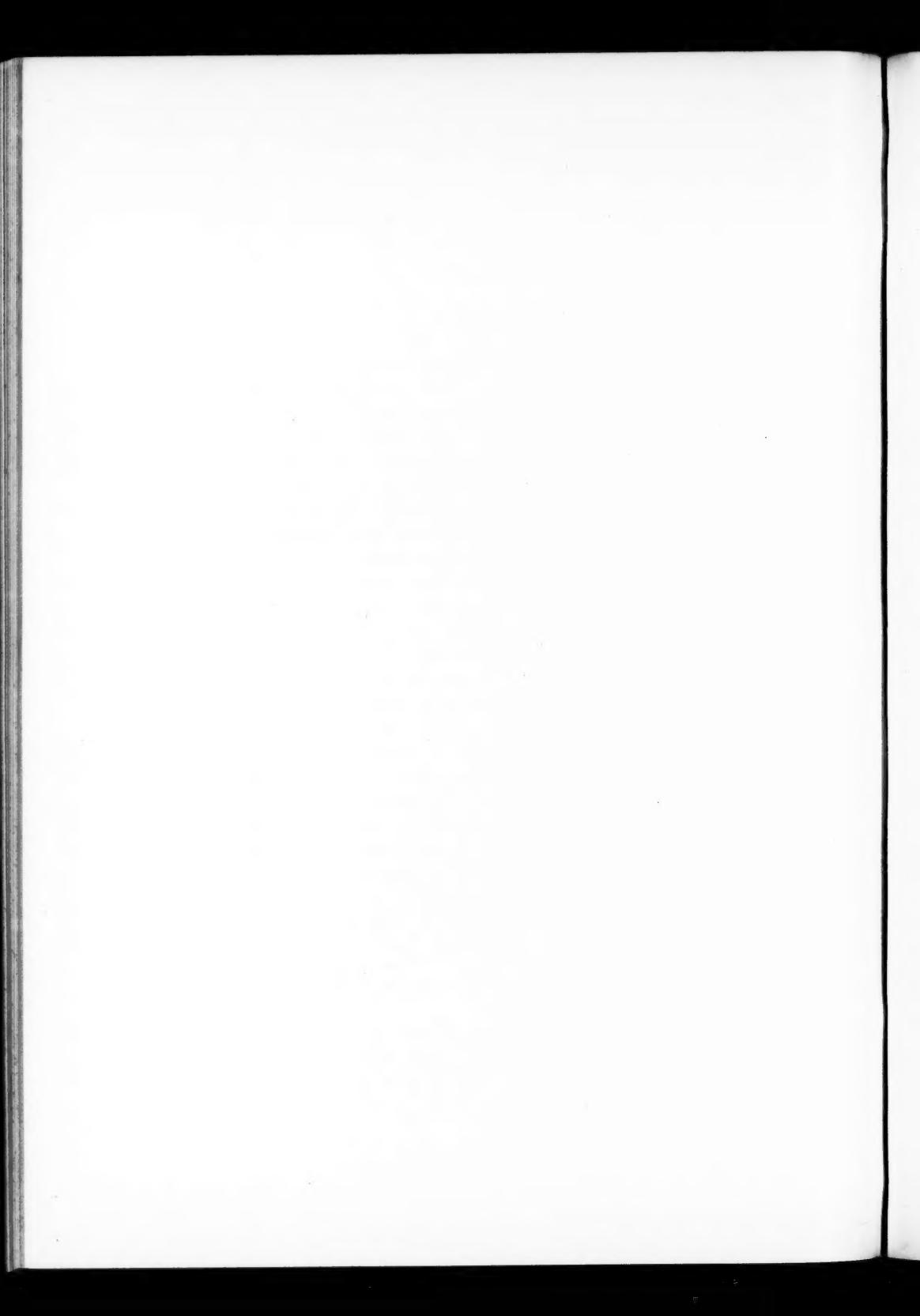
¹ As representative of the 'highest authorities' on this subject I would include the *Standard Dictionary*, the *Century Dictionary*, Murray's *New English Dictionary*, and such special works as Newton's *Dictionary of Birds*. Webster's 'International' and other older dictionaries will not always be found in accord with the authorities just named in compounding words, nor with these rules.

ary, nor in all combined, perhaps; neither do these authorities cited always agree in compounding words, just as they do not always agree in spelling and pronunciation; but they are the best reflectors of good usage we have. In fact, the chief function of the dictionary is to exhibit the usages of the best speakers and writers.

There is one phase of the question on which it is somewhat difficult to secure uniformity. Compound words are divided into two classes: (1) separable compounds, written with the hyphen, as 'tent-caterpillar'; and (2) solidified compounds, written without the hyphen, as 'ladybird.' It is not easy to formulate rules for determining just when the hyphen may be omitted from a compound, and the word written solid. Generally the old and familiar forms are solidified, while the newer and unfamiliar names retain the hyphen; but age and frequency of use alone can not determine. However, this is not so important as some other phases of the subject. Words are compound whether hyphened or solid, and the choice of forms depends more upon taste, since no fundamental language-principle is at stake. But we should strive for uniformity in this respect also. The limits of this paper will not admit a fuller discussion of this feature.

There should be some concerted attempt to secure uniformity in writing the vernacular names of animals. The principles and rules which govern in these matters are just as binding with regard to the hyphen as with regard to capital letters, punctuation, or the construction of sentences. There is no more reason for a writer's ignoring the correct use of the hyphen than for his ignoring any other essential to good orthography or correct syntax.

CHAMPAIGN, ILLINOIS.



NOTES AND LITERATURE

ZOÖLOGY.

“American Food and Game Fishes”¹ is the title of an admirable volume of about 600 pages, written by Dr. D. S. Jordan, President of Leland Stanford University and Dr. B. W. Evermann, Ichthyologist of the U. S. Fish Commission.

This book is the only attempt yet made to give an account of all the species of American fishes north of Panama used by man as food or sought by anglers for the sport which their capture affords. About 1000 species of fish are described, nearly half of which are illustrated by colored plates, half-tones and text figures. The text figures are excellent reproductions from drawings which were originally used to illustrate the species in more technical papers, and are as exact as it is possible to make them. The same is true of the colored plates. The half-tones, of which there are more than 100, are made from photographs of live fish in the water. They were made expressly for this work at Key West, Lake Maxinkuckee, and the Pan American Exposition at Buffalo. The artistic skill displayed in making these photographs has certainly not been excelled in the line of animal photography. The half-tone reproduction of these photographs is seldom equalled.

The fact that the book is written by two of our most active students of American fishes is a guarantee of its excellence. The important feature of the entire book is its accuracy. The descriptions of the different species, their life histories and geographic range are correctly as well as interestingly given.

It is the only book that gives the commercial fisherman accurate and detailed information about all American fishes which find their way into our markets. As a literary and scientific production one cannot praise this book too highly. It is certainly the work of masters. Zoologists will no doubt regret that room was not found

¹ Jordan, D. S. and Evermann, B. W. *American Food and Game Fishes*. A Popular Account of all the Species found in America North of the Equator, with Keys for ready Identification, Life Histories, and Methods of Capture. New York, Doubleday, Page & Co., 1902. 8vo, 1 + 573 pp., plates and text figures.

in the book for an account of the gar pike and the dogfish or *Amia* because of their special interest in these fishes. They are, however, neither food nor game fishes, and are so well known in special works in zoölogy that ready reference to them can easily be had elsewhere.

While this work will not fail to interest the general reader, it will be most highly appreciated by those who really wish to know fishes. To the students of natural history in our high schools and colleges the book will be especially useful, as it is a strictly up-to-date systematic treatise and contains a vast amount of accurate natural history information. By means of keys, descriptions and the illustrations any student of ordinary intelligence can easily identify all of our food and game fishes which he may have.

To the angler it is indispensable, for it tells him where the different game fishes are to be found, and will enable him to readily identify any fish he may catch, and to know it by its correct scientific as well as its common name.

S. E. MEEK.

Notes on Recent Fish Literature.—In connection with the elaborate investigation of the fishes and fisheries of the Hawaiian Islands, undertaken by the United States Fish Commission in 1901 and 1902, Messrs. Jordan and Evermann, who have the work in charge, have published accounts of part of the new species obtained. In this preliminary paper (*Bull. U. S. Fish. Comm.* for 1902) 56 new species are described. These will be figured with all the known species in a final report. The Hawaiian Fauna is much less rich in the species than that of Samoa, and while the Genera are all distinctly tropical, the species are very largely different from those found in Polynesia and Micronesia. This isolation of the Hawaiian Fauna is in part explained by the direction of the ocean currents, which set to the eastward in Samoa and Tahiti, but to the westward about Hawaii. The new Genera in this paper are the following: *Fowleria* (*Apogonidæ*), *Bowersia* (*Lutianidæ*), *Verriculus* (*Labridæ*) *Quisquilius* and *Vitraria* (*Gobiidæ*), and *Osurus* (*Pteropraridæ*).

In the *Annals and Magazine of Natural History* (Vol. II, No. 63), Mr. C. Tate Ragan of the British Museum gives a review of the angler fishes of the family of *Laphiidae*. Three genera are recognized: *Chirolophius* (*naresi*), *Lopheonius* and *Lophius*. *Lopheonius spelurus* Garman, from off Panama, is referred to *Chirolophius*. The species described by the present writer from Japan as *Lopheonius litulon*, is as Ragan suggests, a true *Lophius*, having 27 vertebræ,

while the other Japanese species, externally extremely similar, *Lopheonius setigerus* has but 17 or 18. The former is a species of northern distribution. It is remarkable that so great a difference in the vertebral column should be developed without any considerable external distinction. About 15 species of anglers are now known.

Dr. Tarleton H. Bean has published a useful account of the habits and distribution of the fishes found on Long Island. It occurs in the *Annual Report of the Forest, Fish and Game Commission of New York, 1901*.

A new writer on Ichthyology, Senhor Alipio de Miranda Ribeiro, gives an account of eight fishes from Rio Pomba in a report of the *Sociedade Nacional de Agricultura* for 1902. For the genus usually called *Centropomus*, Ribeiro uses the name *Platycephalus*, "in observance of the laws of priority."

Mr. Cloudsley Rutter, naturalist of the "Albatross," describes the fishes obtained by him in the lakes of North Eastern California (*Bull. U. S. Fish Commission* for 1902). Most of these lakes are without outlet, although formerly tributary to the post-glacial Lake Lahontau. The new species are *Pautorteus lahontau* from Susan River, *Chasmistes chamberlaini* from Eagle Lake, and *Agosia robusta* from Susan River and other streams.

Mr. Rutter also gives a report (*Bull. U. S. Fish Commission* for 1902), on five years' work (1896-1901) of observation on the habits of the Sacramento salmon. It is a very complete and valuable piece of work. Among the important conclusions are these:—

There is no evidence that salmon returning to spawn seek their native stream. Probably most salmon do not wander far into the sea, and the native river is the nearest one when the spawning season comes. There is no evidence that they remember any particular branch of the river basin in which they were spawned. Most salmon return to spawn after two years in the sea, some remaining three and others four years.

All die after spawning, none making any effort to return to the sea. Most of them die within 5 to 16 days after reaching the spawning grounds. They will not survive if placed in salt water. The Pacific salmon are like cast off leaves of a tree, when their period of usefulness to the species is past.

In the *Proceedings of the United States National Museum* (Vol. XXVI) Messrs. Jordan and Fowler continue their discussions of

Japanese fishes. The Elasmobranchs, or sharks, rays and chimæras are represented by 56 species. Other papers are on the Cobitidæ or Loaches, six species in Japan, and on the Cepolidæ or Band-fishes, of which Japan has three. The genera, *Embolichthys* and *Zen* are subjects of a special paper.

In the *Annotationes Zoologicae Japonenses* (Vol. IV) of the Imperial University of Tokyo, Dr. Bashford Dean gives an account of the cleavage of the egg in the cestraciont shark *Heterodontus japonicus*. He finds on the egg certain marks or lines reminiscent of holoblastic cleavage.

D. S. J.

Gardiner's "Maldive and Laccadive Archipelagoes," Part IV.¹—The fourth part of Gardiner's Fauna and Geography contains seven papers including a detailed description, with charts, of the Atolls and Banks—a valuable contribution to geography but not abstractable. In his concluding notes Gardiner touches on the causes of deaths of parts of the coral reefs. Silting up is destructive and senile decay, after the colony has reached a great size, causes great mortality.

The Cephalochorda are described systematically and anatomically by C. F. Cooper while R. C. Punnett considers their variation. A new species, *Heteroleuron maldivense* is described. In the conclusions as to the great variability of Cephalochorda based on the number of myotomes the possibility of an increase in the number of myotomes throughout life is not sufficiently considered.

The Avifauna is analyzed by Gadow. Twenty-six species were examined; none peculiar to the islands. The permanent residents are, excepting the Indian crow, *Corvus splendens*, all water birds, mostly of wide distribution in the Old World. Eight genera of birds are winter visitors from the Asiatic continent and a few species are wanderers from India and Ceylon. Finches, starlings and pigeons are wholly absent. At one point in the Archipelago it was observed that all birds retired daily from 11 A. M. to 3 P. M.

The earthworms are reported upon by Beddard. He comments on the favorable material afforded by this group for studies in geographic variation owing to impracticability of their unassisted migration over a tract of sea. Three species are recorded, two are very common

¹ *The Fauna and Geography of the Maldive and Laccadive Archipelagoes*, etc. Edited by J. Stanley Gardiner. Cambridge University Press, 1903. Vol. i, pt. iv, pp. xix+348-471, pls. 18-25, text figs. 76-119.

and widespread oriental species; the third is a new *Pontodilus* — a seashore inhabitant.

The classification of crabs is undertaken by Borradaile, who thereupon describes the crabs from the Archipelagoes belonging to the Catometope and Oxystomata. As before, especial stress is laid on bionomics and adaptations. A collection of 16 species of Barnacles is also described. Most of them are Indo-Pacific species, but two occur in the West Indies. Lanchester's study of the Stomatopods, based as it is on the study of individual variation will be of interest and, it is hoped, of instruction to the species splitter. Excepting two specimens of *Pseudosquilla ciliata* all the adults belong to the worldwide *Gonodactylus chiragra*, including seven synonyms. *Gonodactylus* lives on the surface of reefs and is abundant here. *Squilla*, which demands mud to burrow in, is absent; because the mud is. This is another illustration of the law that the habitat of a species is determined by its instincts. The author introduces "term" to express the extremes of structural type in a continuous variation.

Finally the Lithothamnia are described by M. Foslie, who combats the erroneous notion that these Algae are more abundant in tropical than in northern seas.

C. B. D.

Webster's "Diffusion of Insects in North America."—In the April number of *Psyche* we have a very interesting article on the above subject, from the pen of Professor F. M. Webster, who has already contributed various papers of the same general nature to our entomological journals.

The problem of the nature and extent of destruction of life during the Glacial epoch is but barely touched upon, the intention of the author being to show how post-glacial distribution has been accomplished. He points out that with the retreat of the ice three gateways for the introduction of species into this continent were open — (1) the Alaskan chain for Asiatic insects, (2) Central America for forms from South America, and (3) Florida, by way of the West Indies as an alternative to the Central American route. All new life depending to any large extent upon land for its introduction must come by some one of these three roads, the agency of man in the matter being of so recent an origin as to need separate consideration.

The northwestern gateway, leading from Asia, seems to have been taken advantage of by numerous Coccinellidae and certain Chrysomelidae.

lidæ. Some of these have a much more extended range in this continent than in the Old World, *Lina lapponica* for example being found as an European species only in the extreme north, while with us it reaches south as far as Texas. This adaptability is a potent factor in distribution and the readiness with which a given species assimilates with new surroundings has a powerful bearing upon its final geographical range. Insects coming to us from Asia by the path mentioned may spread to the south through the great valleys lying between the Rocky Mountains and the Cascades or by use of the passes in the former range gain the great plains of Canada and eventually appear on the Atlantic coast. If their nature is such as to enable them to bear an arid or warm climate they may reach points far to the south since there are no great natural barriers in the way.

The southwestern gateway is, in Professor Webster's opinion, by far the most important since through it we receive accessions from the rich fauna of Central and South America. As a striking example of a fauna received through this medium he cites *Halisidota*, a genus of moths apparently South American in type. Some of our forms are supposed to have had their origin in the South and to have come to us by way of Central America. A certain species with a present range from Argentina to Costa Rica is thought to be the stem of our *H. tesselaris* and *H. citripes*, which seem to have reached us by two different courses—the one coming north by way of Texas, the other east by way of Yucatan and Cuba. The distribution of Pacific and northern *Halisidotæ* indicate to the author the probability of certain species having reached (through stem forms) the New England coast by following the Pacific Maritime trend from Central America through California, Oregon, Washington and British Columbia, thence traveling eastward along the lines indicated for the immigrants of Asiatic origin. The genus *Diabrotica*, among the beetles, warrants the belief that offshoots of a common Central American stem may become separated far to the south, one going to the Pacific district while its fellow inhabits the Atlantic slope.

But little matter concerning the antillean trend is presented, this being thought of less importance than the others, though many insects appear to have come in that way.

Concerning the route taken by insects introduced through the eastern ports by agency of man, Professor Webster has ascertained that they follow a path which he calls the transappalachian trend—reaching the fertile prairies of the interior through the great gap in New York which forms the principal thoroughfare for insect invasion.

A glance at the map with which the paper is illustrated suggests the thought that we have in Professor Webster's article a strong defense of the Wallacean theory of distribution and of the important part played by barriers in determining the spread of animal life; it is to be regretted that the recent propaganda of the theory of isothermal distribution of organisms, while undoubtedly of great value in indicating the possibility of artificial cultivation, has tended to obscure the importance of geographical features under really natural conditions.

H. F. WICKHAM.

BOTANY.

Livingston's Osmotic Pressure and Diffusion in Plants.¹ — The author begins with a treatment of the purely physical phenomena connected with diffusion and osmosis, rightly holding that it is difficult for the student of physiology to easily obtain the information he needs in compact form. Such a treatment covering, as it does but forty-four pages could not possibly be detailed, nor does the author maintain that it is. Nevertheless a summary of this kind can be exceedingly useful, if in no other way than to stimulate the student to further reading. This *r  sum  * is clear and sufficiently full to give an adequate conception of the theories concerned. There are six chapters in the first part, which treat of the fundamental theories of the nature of matter, of diffusion and diffusion tension, of solutions and ionization, of osmotic phenomena and the measurement thereof.

In the second part on the physiological aspect of the matter, the author continues his summarization of the work which has been done, but of course in far greater detail than in the previous half, since the field is smaller and since this is the real object of the book. In the first chapter the question of turgidity is taken up. The importance of this subject demands full treatment, and forty-two pages are devoted to it; the author does not develop anything new, however. In the even more complicated, and certainly more dubious, matter of the absorption and transmission of water, which is consid-

¹ Livingston, Burton E. *The Role of Diffusion and Osmotic Pressure in Plants*. The Decennial Publications of the University of Chicago. Second Series, vol. 7. The Univ. of Chicago Press, 1903. 8vo, pp. i-xiii, 1-149.

ered in the second chapter, there is hardly space enough allowed for a very complete discussion of the question. The optimistic point of view is taken that when the nature of the plasmic membranes is known, "it is not improbable that the solution of the problem of water transport will follow as the simplest corollary." In the next chapter the absorption and transmission of solutes is treated of, the important matter of quantitative selection is somewhat lightly referred to, and one is lead to the belief that it is either taken as a matter of course, or that the author does not consider it of the same importance that many physiologists do. Simple diffusion is said to be the greatest factor in the distribution of solutes in the plant body. As to the influence of the osmotic pressure of the surrounding medium upon organisms, which is the subject of the final chapter, the author gives a summary of his own work in that line and of that of other investigators. Investigations have shown that growth is accelerated in weak solutions of various substances and retarded in concentrated ones. Cell division may also be influenced by the osmotic pressure of the surrounding medium, and reproduction being a peculiar form of cell division is apparently dependent, in some cases, upon the pressure. Whether the effect is due merely to the extraction of water, or to a strictly chemical influence the author does not decide.

While there is not a great deal that is new in the volume it is an excellent brief review of the various questions as they stand to-day. As a reading book for more advanced students in physiological botany the book will have considerable value, and it is one which may well be placed upon the shelves of the laboratory reference library. As a final source of information it cannot of course be satisfying, but the copious references to the literature make it valuable in this respect also. There is a distinct place for a book of this character.

H. M. R.

Pierce's Plant Physiology.¹—In his preface the author expresses his desire to fill the gap in text books which exists between the monumental work of Pfeffer on the one hand, and the clever but short account of plant physiology which is found in Stasburger's text-book. The intention to furnish a good reading book of this character is certainly a laudable one, and in so far as the author has succeeded, he is to be congratulated. It is further stated that only "safe views"

¹ Pierce, G. J. *A Text-Book of Plant Physiology.* New York, Henry Holt & Co. 1903. 8vo., vi-291 pp., 22 figs.

of the various physiological processes will be given, and such a position may also be regarded as an excellent one. Too great conservatism, however, may easily lead to two serious difficulties, one is that the style may readily become unsuggestive and the other is that these very same "safe views" may become almost dogmatic. After an introductory chapter on the general problem of physiology the question of respiration is at once entered into and with it the correlated phenomena of fermentation. There may be some who would be inclined to doubt the entire wisdom of at once plunging into these complicated matters, before the student has been informed of what is known as to how or where the materials concerned in respiration are produced. This is especially true of the subject of enzyme action, and as a consequence the handling of this important topic is hardly satisfactory.

The space devoted to it is chiefly taken up with a consideration of yeast fermentation, and the great classes of intra-cellular enzymes are scarcely mentioned. The third chapter is on Nutrition and in the next, absorption of water and food is treated of. Here for the first time the fundamental question of osmosis is explained. The different, necessary chemical elements, are taken up in turn. In passing it may be mentioned that the literature quoted does not always include the latest contributions to the subject, by the authors named. The fifth chapter is devoted to the consideration of the primal phenomena of growth, and following it is a long one, entitled Irritability, under which head all growth responses, as well as the movements of nature organs, are taken up. As an example of unfortunately dogmatic statements may be mentioned the following, which is given as an explanation of phototropism: "The cells on the side of the stem away from the window receive less light and are less checked than those on the opposite side, and hence push the tip of the stem over towards the window." Such a definite explanation, on the basis of etiolation, as the cause of phototropic curvature would not be accepted by many physiologists, and is perhaps too "safe" a view to take of this perplexing response. Attention may also be called to the fact that the familiar term, etiolation is not used at all by the author, and that the term heliotropism is preferred to the generally admitted better one, phototropism. The last chapter deals in the compass of thirty pages with the subject of reproduction, including a three and one half page consideration of the problems connected with heredity. The index leaves something to be desired, not infrequently one must look in vain for references to familiar terms, such as hyponasty, epinasty, etiolation, etc.

It is perhaps unfair to the book to have picked out such passages, where the handling of the subject is not in accord with the ideas of the reviewer although many more might be cited. In the main it is a careful and conservative — almost too conservative — treatment of the subject of plant physiology. According to one's point of view, its faults or its virtues lie in the very definite, perhaps non-stimulating style, in which it is written. It will no doubt prove a useful addition to the somewhat slim stock of reading books in plant physiology which are at the disposal of the English reading student.

H. M. R.

Notes.— *The American Botanist* for April contains the following articles:— Bailey, "Violets"; Bradshaw, "The Chillicothe Vine"; Blight, "What is American Weed?"; Fetherolf, "Among Texas Ferns"; and Steele, "Species or Varieties?"

Part IX of *Hough's American Woods*, published at Lowville, N. Y., comprising nos. 201 to 225 inclusive of his admirable sets of radial, tangential, and cross sections of each species, is devoted to Pacific Coast species, and is accompanied by a text brochure including, in addition to an account of each of the species represented in this part, leaf and fruit keys to the entire series thus far issued.

The Botanical Gazette for April contains the following articles:— Davis, "Oogenesis in *Saprolegnia*"; Mottier, "The behavior of the chromosomes in the spore-mother-cells of higher plants and the homology of the pollen and embryo-sac mother cells"; Hitchcock, "Notes on North American grasses—III, New species of *Willkommia*," and Bower, "The morphology of spore producing members."

The Bryologist, for May, contains the following articles:— Grout, "Some interesting forms of *Polytrichum*"; E. G. Britton, "Notes on nomenclature—II"; Bailey, "An interesting tree"; Grout, "Sun prints in bryology—additional notes"; Holzinger, "Obituary, M. Emile Bescherelle," and "*Scligeria tristichoides* in southern France"; and Williams, "*Oxipodium Griffithianum*."

The Bulletin of the Torrey Botanical Club for April contains the following articles:— Goebel, "Regeneration in plants"; Morgan, "The hypothesis of formative stuffs"; Howe and Underwood, "The genus *Riella*, with descriptions of new species from North America and the Canary Islands"; Murrill, "The Polyporaceae of North America—III, the genus *Fomes*"; Piper, "Four new species of grasses from Washington"; Osterhout, "New plants from Colo-

rado"; Eastwood, "New species of *Oreocarya*"; and Rydberg, "Studies on the Rocky Mountain flora—X."

The *Bulletin for the Torrey Botanical Club*, for May, contains the following articles:—Rydberg, "Some generic segregations"; Harper, "Botanical explorations in Georgia during the summer of 1901—I"; Murrill, "The Polyporaceae of North America—IV, the genus *Elvingia*"; Kunzé, "The desert flora of *Phoenix*, Arizona"; and Sheldon, "New species from the Pacific Coast—I."

The Fern Bulletin for January, with portrait of J. A. Graves as frontispiece, contains the following articles:—Clute and Cocks, "The fern flora of Louisiana"; Waters, "My indoor fernery"; Eaton, "The genus *Equisetum* in North America, XII, the sub-genus *Hippochaetae*"; Clute, "Fernwort notes—I"; Buchheister, "Notes from the Catskills"; Cocks, "*Equisetum robustum*"; Flett, "Variations in the habitat of two ferns"; Clute, "Cultivation of our hardy ferns"; and Anthony, "Notes on the ferns of Florida, East Coast."

The Fern Bulletin for April, with portrait of R. R. Scott as frontispiece, contains the following articles:—Reverchon, "The Fern flora of Texas"; Maxon, "Notes on American Ferns—VI"; Eaton, "The genus *Equisetum* in North America—XIII: *E. levigatum*"; Osmun, "*Equisetum scirpoideum* in Connecticut"; Clute, "Fernwort notes—II"; Eaton, "Raising *Nephrolepis* from spores"; Druery, "New forms of Ferns"; and Clute, "List of Fernworts collected in Jamaica—conclusion."

Under the title *Flora and Sylva*, Mr. Robinson, an enthusiastic student and cultivator of plants, has begun the publication of a new monthly journal, beautifully illustrated. The editorial offices are at 63 Lincoln's Inn Fields, London. The first number contains exquisitely colored plates illustrating species of *Magnolia* and *Calochortus*.

The *Journal of the New York Botanical Garden* for May contains, among other things, reports on a trip to eastern Cuba; the Jenman collection of ferns; and a large collection of conifers for the pinetum of the institution.

Like earlier volumes, the fiftieth volume of *Proceedings of the American Pharmaceutical Association* contains a considerable number of scientific papers dealing with the structure and particularly active principles of plants which furnish medicinal products.

Rhodora, for May, contains the following articles:—Collins, “Lorin Lowe Dame”; Blankinship, “Plant formations of eastern Massachusetts”; Sargent, “Recently recognized species of *Crataegus*—III”; Bissell, “*Ajuga Genevensis* in New England”; Fernald, “Red-flowered *Anemone riparia*”; and Robinson, “*Viola arvensis* in New England.”

Torreya, for April, contains the following articles:—House, “Notes upon the orchids of central New York”; Ross, “Vagaries of *Hepatica*”; Earle, “Key to the North American species of *Lentinus*—II”; and King, “Explosive discharge of antherozoids in *Conocephalum*.”

Torreya, for May, contains the following:—Harshberger, “Notes on the strand flora of Great Inagua, Haiti and Jamaica”; Curtis, “Observations on etiolation”; and Berry, “A triple samara in *Acer rubrum*.”

Part 2 of *Trees and Shrubs*, issued from the Riverside Press of Cambridge, like its predecessor contains illustrations and descriptions of a number of species of the now popular genus *Crataegus*, as well as of other genera of interest.

In the *Bulletin de l' Herbier Boissier*, Dr. Hallier has recently published a preliminary scheme for a new phylogenetic classification of the flowering plants. Dr. Engler, in the new edition of his *Syllabus*, also considerably modifies his previous treatment of the larger groups.

A practical application of the various ways of treating botanical nomenclature is given by Hitchcock, apropos of *Festuca spicata*, Pursh, in *Science*, for May 22, 1903.

An important, though not lengthy, paper by Van Tieghem, on the structure of the stamen in Serophulariaceae, is contained in No. 8 of the *Bulletin du Muséum d'Histoire Naturelle*, for 1902.

The Morphological propriety of designating stamens and pistils sexual organs, is discussed by Ganong in *Science* of April 24, and MacMillan in the same journal for May 15.

Cotyledonary studies of *Pinus maritima*, by Chauveaud, are published in No. 7 of the *Bulletin du Muséum d'Histoire Naturelle*, for 1902.

Ramaley has a note on the cotyledons and leaves of certain Papilionaceæ, in No. 3 of *The University of Colorado Studies*.

The *Botanische Zeitung* of April 16 is occupied by an analysis of recent hybridization literature, by Correns, who also contributes two papers on the same subject to the *Berichte der Deutschen Botanischen Gesellschaft* of April 23.

Professor Fernow has an article on "applied ecology" in *Science* of April 17.

"New Hampshire Wildflowers" is the title of *Nature Study Leaflet No. 4* of the New Hampshire College Experiment Station, by Professor Weed.

An account of a biological reconnaissance in the vicinity of Flathead Lake, by M. J. Elrod, is published as No. 10 of the *Bulletin of the University of Montana*,— No. 3 of the biological series.

Professor Ganong contributes a preliminary synopsis of the grouping of the vegetation (phytogeography) of the Province of New Brunswick to No. XXI of the *Bulletin of the Natural History Society of New Brunswick*.

A list of plants from Labrador, by Mackay, is contained in the *Proceedings and Transactions of the Nova Scotian Institute of Science*, Vol. X, part 4, issued in March.

An account of the vegetation of one of the Amazon districts, by Huber, is published in the December number of the *Boletim do Museu Paraense*, and includes 189 entries. The article is followed by an account by the same author of the physical geography of the region, the "Furos de Breves" or communications between the Amazon and the Para.

With the third fascicle, issued under date of January, 1903, De Wildeman's *Études sur la flore du Katanga*, constituting "Series IV — Botanique" of the *Annales du Musée du Congo*, is completed. The work forms a folio volume of xii + 241 pages, and 46 plates.

A monograph of Cardamine, by Schulz, has recently been published in Engler's *Botanische Jahrbücher*.

Under the title "Leguminosæ Langlasseanæ" the *Société de Physique et d'Histoire Naturelle de Genève* has published, as Volume XXXIV. Fascicle 3, of its *Mémoires*, a beautifully illustrated account of certain Leguminosæ collected in 1898 and 1899 by Langlasse through the Mexican states of Michoacan and Guerrero. The man-

uscript was prepared, shortly before his death, by Micheli, whose portrait forms a frontispiece to the paper.

A short note on New Brunswick violets, by Vroom, is printed in no. XXI of the *Bulletin of the Natural History Society of New Brunswick*.

A critical revision of the genus *Eucalyptus*, by J. H. Maiden, Government Botanist of New South Wales, is in course of publication at Sydney. The first part, comprising 47 pages of text and 4 plates, bears date of January, 1903, at end of the preface.

"A research on the Eucalypts, especially in regard to their essential oils," by Baker and Smith, is published from the *Technological Museum* of New South Wales, as No. 13 of the *Technical Education Series* of its publications.

A revision of *Sebaea*, § *Eusebaea*, by Schinz, is distributed from the *Mittheilungen der geographischen Gesellschaft in Lübeck*, Heft 17, 1903.

An analysis of the relationships of the vernal group of *Primula*, comprising the oxlip, cowslip and primrose of England, by Bailey, is printed in *The Journal of Botany* for May.

Betula papyrifera is figured in Vol. IV, no. 1, of the *Icones Selectae Horti Thenensis*, published by M. Leon van den Bossche of Tirlemont, Belgium;—one of the most accurate and attractive of current works devoted to the illustration of the higher plants.

A catalogue of the Mosses of Australia and Tasmania, by Whitelegge has been started, the first part appearing as a supplement to no. 107 of the *Proceedings of the Linnean Society of New South Wales*.

Some points in the structure and life history of diatoms are discussed by F. R. Rowley in an illustrated paper in *The Journal of the Quekett Microscopical Club* for April.

An exhaustive and beautifully illustrated account of "blueing" and "red rot" of the western yellow pine,—caused respectively by *Ceratostomella pilifera* and *Polyporus ponderosus*, is published by von Schrenk as *Bulletin* no. 36 of the *Bureau of Plant Industry of the U. S. Department of Agriculture*.

The synonymy of *Gloesporium fructigenum* is discussed by von Schrenk and Spaulding in *Science* for May 8.

An illustrated account of the coffee disease caused by *Stilbella flavida*, is published by Kohl in the *Beihefte zum Tropenpflanzer* for May.

A destructive apple rot, caused by *Cephalothecium roseum* following the attacks of *Fusicladium*, is described by Eustace in *Bulletin of the New York Agricultural Experiment Station* No. 227, and the preceding Bulletin of the same station deals with the obscure cane blight and yellows of the raspberry.

What appears to be an important study of the cancer of trees, referred to a bacterial cause, by Brzezinski, is contained in the March number of the *Bulletin International de l'Académie des sciences de Cracovie, classe des sciences mathématiques et naturelles*.

Dr. G. U. Hay, in No. XXI of the *Bulletin of the Natural History Society of New Brunswick*, records over 180 species of higher fungi for that Province, in addition to an earlier list which is reprinted.

An important paper on the Algae of northwestern America, illustrated by eleven plates, is published by Setchell and Gardner in Vol. I. of the *University of California Publications — Botany*, issued on March 31.

The Hokkaido governmental fishery bureau is publishing in Japanese a well illustrated series of reports on the marine resources of Hokkaido, the third of which deals with the Laminariaceæ and Laminaria industries.

Under the title "The Fower Beautiful," Professor Weed has written an attractive and daintily illustrated little book on the decorative use of flowers, published by Houghton, Mifflin & Co., Boston.

An article on the forest policy of Pennsylvania, by G. W. Wirt, is published in the *Journal of the Franklin Institute* for May.

Some useful shade-tree suggestions, for Wyoming, are published by Aven Nelson as *Bulletin of the Agricultural Experiment Station*, no. 57, of that state.

An economic account of *Manihot*, by Tracy, forms *Farmers' Bulletin of the U. S. Department of Agriculture*, no. 167.

An account of olives and olive oil in France, by R. P. Skinner, is published as no. 1639 of *Advance Sheets of Consular Reports*, dated May 6.

The Kumquat and Mandarin groups of Citrus are discussed by Hume in *Bulletin of the Florida Agricultural Experiment Station*, Nos. 65 and 66.

Some conditions of stock poisoning in Idaho are discussed by Professor Slade in *Bulletin of the Experiment Station*, No. 37, of that state.

The poisoning of cattle by *Sorghum vulgare* is considered by Peters, Slade and Avery in *Bulletin of the Agricultural Experiment Station of Nebraska*, No. 77.

The first volume of "Datos para la materia médica argentina," by J. A. Dominguez, has been issued by the Museo de Farmalogía of Buenos Aires.

The value of making an herbarium is the subject of an article by Cameron in *School Science* for May.

"More Letters of Charles Darwin," published by the Appletons (New York) in two volumes, contain a number of letters of interest to botanists.

CORRESPONDENCE.

To the Editor of the American Naturalist:

SIR:—A little over a year ago Dr. William Patten¹ claimed to have discovered evidence of "numerous pairs of jointed oarlike appendages" in Tremataspis and related forms, in none of which had similar indications been previously detected. Nor, for that matter, had anyone previously had the temerity to attribute more than two pairs of limbs to any vertebrated creature, living or fossil. Beyond Dr. Patten's assertion that Cephalaspis is provided with "a fringe of jointed and movable appendages (25-30 pairs) along the ventral margin of the trunk," we have had from him no further enlightenment as to the ambulatory equipment of this Ostracophore, but there has recently been heard from Dr. Gaskell² an absolute denial of the existence of segmental appendages in that genus.

Now, since it appears that segmented appendages are wanting not only in Cephalaspis, but universally amongst the Heterostraci and Osteostraci so far as known, the presumption is certainly very strong that they do not occur in Tremataspis, whose close relationship with Cephalaspis none will question. Professor Patten, however, in returning to the matter *de novo*,³ combats against this presumption, and affirms his belief in the existence of not only one, but possibly *several* pairs of jointed appendages in Tremataspis. Naturally he must have strong reasons for inclining him to so heterodox a notion, and what are they, palaeontologists are curious to know? Has he discovered specimens showing one or more pairs of these chimærical organs

¹ On the Structure and Classification of the Tremataspidæ. *Amer. Nat.*, vol. 36. 1902, pp. 379-393.

² On the Origin of Vertebrates, *Journ. Anat. and Phys.*, vol. 37. 1903, p. 198, text fig. 5.

³ On the Appendages of Tremataspis. *Amer. Nat.*, vol. 37. 1903, pp. 223-242.

in situ? Or has he found detached appendages positively determinable as belonging to *Tremataspis*, to the exclusion of all other accompanying fossil remains? Professor Patten answers the first of these interrogatories in the negative, the second affirmatively. He has obtained in all four detached plates of small size and mediocre preservation, which he regards as portions of as many "paired cephalic appendages"; these he figures of ten times the natural size and describes in praiseworthy detail. But by what process of reasoning he is able to identify them as belonging indubitably to the genus *Tremataspis* he does not take the trouble to state, leaving the reader to take it for granted that his determination is correct.

Not all readers, however, will be prepared to accept a determination so utterly at variance with analogy. On the contrary, rational students will maintain that inasmuch as certain fish fragments are identifiable as parts of jointed oarlike appendages, that fact is *prima facie* evidence of their pertaining not to *Tremataspis*, but to an entirely different order of Ostracophores — the same to which *Pterichthys*, *Bothriolepis* and *Asterolepis* belong. This indeed was the view taken by Pander as early as 1856, who, so far from associating certain fragmentary appendages from the Baltic Silurian with *Tremataspis*, referred them to the *Pterichthyid* order, whose presence in those beds is not otherwise indicated. This procedure is entirely justified by the fact that structures of this nature are known to be present in the group typified by *Pterichthys*, but not in that to which *Tremataspis* and *Cephalaspis* belong. The danger of a reliance on merely superficial characters for the determination or theoretical association of detached fragments is well illustrated by Cope's confusion of an appendage of *Bothriolepis* with *Holonema* remains,¹ certainly no trifling error, and other instances are but all too common. To cite an analogous case borrowed from invertebrate paleontology, it is the same as if Professor Patten had found parts of a *Eurypterus*- or *Pterygotus*-like swimming appendage, and was misled by superficial resemblances into supposing it to have belonged to some genus of *Trilobites*.

¹ On the Characters of some Palaeozoic Fishes. *Proc. U. S. Nat. Mus.*, vol. 14. 1891, p. 456, pl. XXX, fig. 7.

occurring in the identical formation, and exhibiting similar texture or surface markings. We wonder how many would be converted to this belief until a Trilobite had first been discovered with the actual members preserved *in situ*?

In precisely the same way we must reject Professor Patten's theoretical association of parts as erroneous, and deny that forms like Tremataspis, Cyathaspis, Cephalaspis, Tolypelepis, etc., possessed paired segmented appendages until at least one single individual shall have come to light having the postulated organs

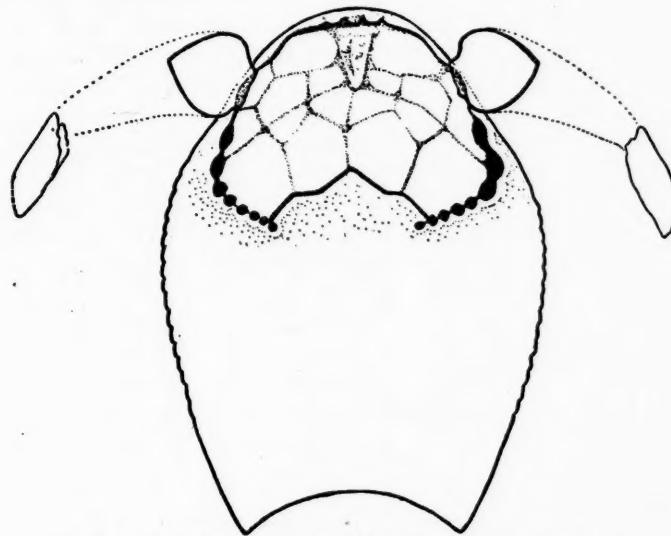


FIG. 1. Ventral aspect of the head-shield of *Tremataspis* (from Patten).

preserved *in situ*. We can also afford to await the discovery of a six- or eight-limbed vertebrate before abandoning a rather deep-seated prejudice in favor of a maximum number of two pairs of limbs.

Professor Patten calls attention to the marginal openings on the visceral side of the head-shield in Tremataspis, arguing that their ventral position furnishes strong reason for believing that they served for the attachment of appendages. But this argument, such as it is, is negatived by the fact that a row of

precisely similar openings occurs in Birkenia on either side of the body at its junction with the head,—that is to say, in a position where they would *not* be serviceable for the attachment of such organs. These openings are commonly regarded as branchial in function, in which case it is easy to conceive of them as having been diaposed in the two genera relatively as in the skate and shark.¹

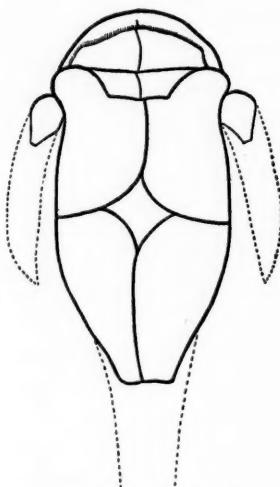


FIG. 2. Ventral aspect of the body-armour of *Pterichthys*.

It is the veriest flight of fancy to suppose that the series of six lateral openings in Birkenia, and nine ventral ones in Tremataspis, imply the existence of as many pairs of segmental appendages in the respective forms. And were we to temper our imagination so far as to conceive that only two pairs of incisions served for this purpose, or indeed even one pair, what function should we assign for the rest, since they are all alike? Given an integral series, why complicate matters by postulating a multiple function? Either let us regard them provisionally as gill-openings, or else declare that their

nature is entirely problematical; Patten's guess we are not prepared to take seriously, even as a guess.

One point further must not escape attention. Our denial of the existence of appendages in Tremataspis is supported not only by analogy and negative evidence, but by the general configuration of the head-shield itself. The latter agrees with that of Cephalaspis, Auchenaspis, Drepanaspis and the like, in its convex or regularly elliptical outline, especially as seen from the ventral aspect, where according to Patten the appendages had their attachment (Fig. 1). But if we examine the visceral surface

¹ Traquair, R. H. Report on Fossil Fishes. *Trans. Roy. Soc. Edinburgh*, vol. 39, 1899, p. 859.

of Pterichthys, Bothriolepis or Asterolepis, we note at once that the contour of the body-wall is inflected, or even indented, on either side at the point where the pectoral limbs peculiar to these forms were attached (Fig. 2). This latter condition being governed by mechanical principles, as anyone can perceive, it is common only amongst those forms which possess swimming appendages. And its absence in Tremataspis and generally throughout the order to which it belongs fortifies us in our conclusion that in this group paired segmental appendages were wanting.

C. R. EASTMAN.

CAMBRIDGE, MASS.

(No. 439 mailed September 5, 1903.)



